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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 83, NO. 3, PP. 183–191 MAY, 1956

CYTOLOGY OF ANDROPOGON DISTACHYUS L

ROBERT P. CELARIER

The exact taxonomic position of the genus *Andropogon* has been a matter of dispute for the past fifty years and there is no indication of a settlement of the issue. However, there are a few species that are considered by one and all to be respectable members of the genus. Outstanding among these is *Andropogon distachyus* L. which is the type for the genus.

A. distachyus L. is widely distributed throughout the Mediterranean Region, most of Africa and is also found in south Arabia. It is quite polymorphic, but no more so than many of the species in this genus. In the small country of Eritrea alone some five subvarieties have been listed by Hackel and Chiovenda (Stapf 1919). Stapf, however, is of the opinion that these represent only ecological types.

It seems quite likely that this is the same species that was studied by Saura (1943) as *Andropogon distachyum* L. This material apparently came from the Maritime Alps of Mediterranean Europe. It was found to have forty somatic chromosomes with twenty bivalents during meiosis.

Materials and methods. All entries were received from their native habitats by collections of either plants or seed. In the case of seed, they were germinated in the greenhouse, transferred as seedlings to individual bands in flats, and later transplanted in the Andropogoneae nursery. This nursery consists of a rather uniform block of land on the Agronomy farm at Stillwater, Oklahoma, so divided as to give a large number of short rows containing 18-20 plants each. All cytological material and herbarium specimens were taken under these uniform conditions. Bud material was fixed in Carnoy's solution and the microspores were smeared and stained in aceto-carmine. Herbarium specimens were taken for all entries and deposited in the following herbaria: Royal Botanic Gardens Herbarium, Kew, England; Missouri Botanical Garden Herbarium, St. Louis, Missouri; University of California Herbarium, Berkeley, California; Smithsonian Institution Herbarium, Washington, D. C.; and the University of Pretoria Herbarium, Pretoria, South Africa.

Results. Four entries were available for this study and all were from the southern shores of the Mediterranean Sea. One, A-4392, was from Tunis, Tunisia, another, A-5422, from near Boulhaut, Morocco, and the other two were from Israel, A-3183 from South Galilee and A-2644 from West Upper Galilee. One entry, A-2644, was analyzed in considerable detail and the others studied only sufficiently to demonstrate that they had similar chromosome behavior.

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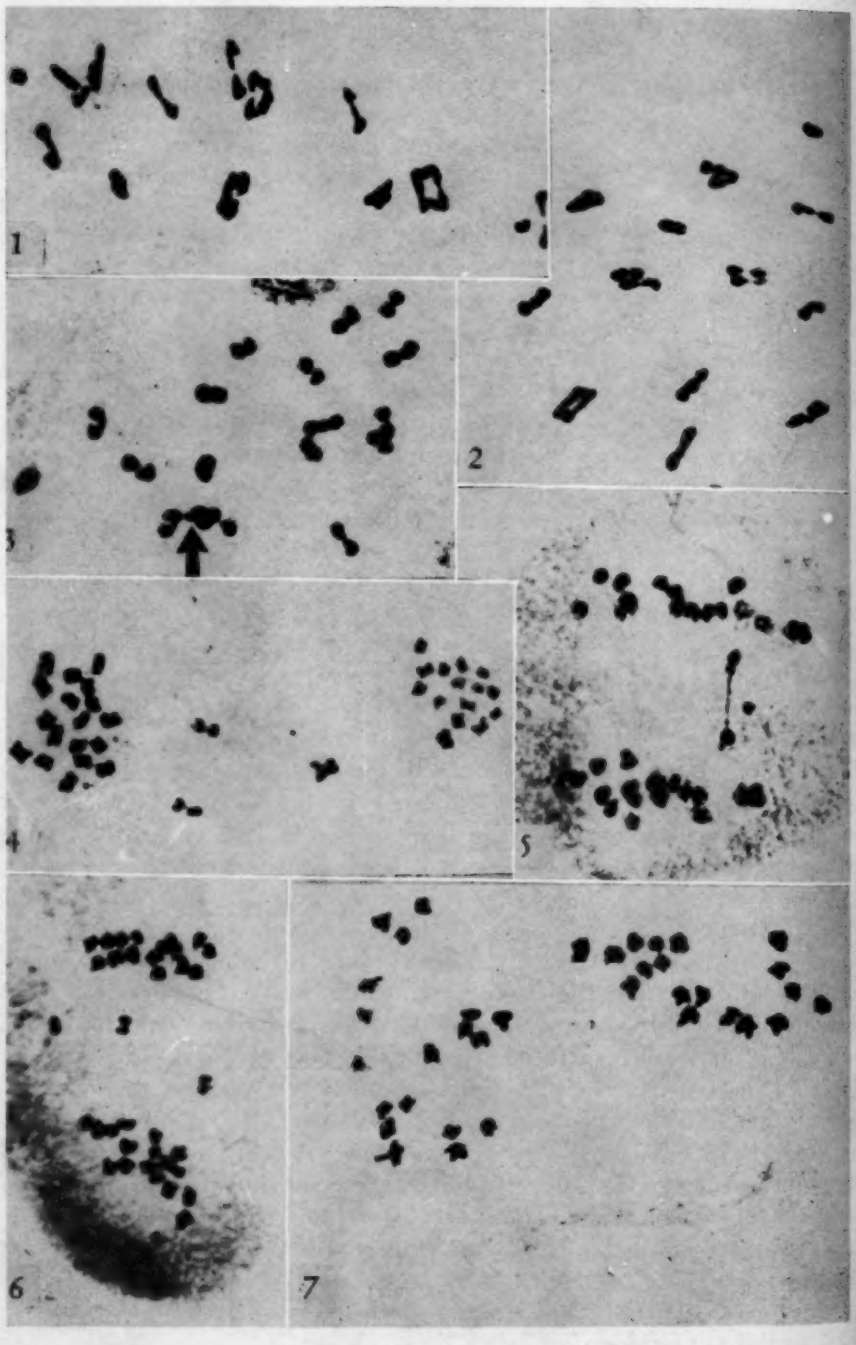
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All entries were found to be 2n = 36 and apparently demonstrate a basic number of 9.

At diakinesis and metaphase I fifty cells of A-2644 were analyzed in detail. Only those cells were used in which all of the chromosomes could be counted with comparative certainty. Univalents, bivalents, trivalents, quadrivalents and one hexavalent were found (figs. 1 and 2) and the results are tabulated in Table 1 (the hexavalent has been omitted). This table gives the ranges of the various configurations as well as the average number per cell.

Almost no cells were seen with 18 bivalents, only one in fifty (fig. 3), and all other cells had at least one quadrivalent. Univalents were present in 23 of 50 cells, and trivalents in seven cells. Although no data were taken on the frequency of rings in the quadrivalents, it was noted that chains were infrequent. The other three entries were similar in their cytological behavior to A-2644 and the deviation observed is quite likely due to the small size of the samples. However, it is of some interest to note that these entries have somewhat more bivalents and fewer quadrivalents per cell than A-2644.

Although there was some variation in chromosome size in the different cells studied they were always comparatively large. This variation in size was no doubt partly due to the particular stage of meiosis studied as well as physical and chemical reactions of the environment in fixation, staining, heating, etc. However, by measuring all cells at a similar condition in metaphase I and by sampling a number of cells, the average size was found to be approximately 5.6 microns.

At anaphase and telophase I there were found considerable irregularities such as unequal distribution of the chromosomes to the daughter cells, lagging chromosomes, and very rarely a bridge + fragment (Table 2).

The chromosome behavior at these stages was analyzed from 134 cells of A-2644. The results showed 64.2% normal cells, 33.6% with lagging chromosomes and 2.24% with a bridge and a fragment (figs. 4, 5, and 6). Very similar results are found when the four entries are averaged (Table 2).

The lagging chromosomes were found to vary in number from one to four with one being common and the other conditions rare. The laggards

FIGS. 1–7. Meiosis in *A. distachyus*. 1350×. FIG. 1. Metaphase I with 2 univalents, 2 tetravalents, one ring of six chromosomes and 10 bivalents. FIG. 2. Metaphase I with 2 univalents, 4 tetravalents and nine bivalents. FIG. 3. Metaphase I with 18 bivalents (three lying together at arrow). FIG. 4. Late anaphase I with three lagging chromosomes and 18 chromosomes at one pole and 15 at the other. FIG. 5. Anaphase I with a bridge and a fragment. FIG. 6. Anaphase I with three lagging chromosomes and 17 chromosomes at one pole and 16 at the other. FIG. 7. Anaphase I with normal 18:18 distribution of the chromosomes to the daughter cells.

TABLE 1. *Chromosome behavior in A. distachyus at diakinesis and metaphase I.*

A-No.	Origin	Collector	Range	Av. no. per cell			
				I	II	III	IV
2644	Matzuda, W. Upper Galilee	D. Zohary	0-6I, 5-18II, 0-2III, 0-6IV	1.20	12.38	0.20	2.40
3183	South Galilee	A. Kamm	0-4I, 12-16II, 0-1III, 0-2IV	2.00	13.80	0.20	1.60
4392	Tunis, Tunisia	Mme. Pottier-Alapetite	0-2I, 10-18II, 0-1III, 0-4IV	0.57	14.07	0.14	1.71
5422	Boulhaut, Morocco	C. Sauvage	0-4I, 11-17II, 0III, 0-4IV	0.64	13.68	0.00	2.00

TABLE 2. *Chromosome behavior in A. distachyus at anaphase and telophase I.*

A-No.	Total No. Cells	Bridges No.	Bridges %	Fragments No.	Fragments %	lagging chromosomes											
						0		1		2		3		4		++lag.		Not++	
						No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
2644	134	3	2.24	3	2.24	86	64.2	37	27.6	7	5.2	0	0	1	0.8	24	45	29	55
3183	21	0	0	0	0	7	33.3	7	33.3	3	14.3	2	9.5	2	9.5	17	63	10	37
4392	25	0	0	0	0	13	52.0	3	12.0	8	32.0	1	4.0	0	0	2	10	20	90
5422	32	3	9.37	3	9.37	14	43.7	13	40.6	3	9.4	2	6.2	0	0	18	72	7	28
Total	212	6	2.8	6	2.8	120	56.6	60	28.3	21	9.9	5	2.4	3	1.4	61	48	66	52

were in all cases univalents and they were found dividing in 45% of the cases and non-dividing in the others. Bridges were never found without fragments so that it is assumed that structural heterozygosity for inversion are present.

The other entries were studied in only a few cells and although differences in frequency of laggers as well as absence of bridges and fragments in two entries were found, it is again felt that this discrepancy is due principally to size of sample.

By combining the data from all four entries it was found that univalents occurred in 39% of the cells. It is seen from Table 2 that the combined data for lagging chromosomes is 43% of the cells with laggards at anaphase and telophase I. Since these figures are very similar it seems probable that at least most of the laggards resulted from unpaired chromosomes at metaphase I.

In a few cells it was possible to count all of the chromosomes at anaphase I and the five major types of distribution to the daughter cells were:

TABLE 3. *Chromosome distribution at anaphase I*

A-No.		18:18	17:19	17:1:18	17:2:17	16:2:18	Others	Total No. Cells
2644		22	7	12	2	1	4	48
3183		6	1	3	1	1	1	13
4392		9	1	1	2	0	1	14
5422		3	1	4	1	0	1	10
Total	No.	40	10	20	6	2	7	85
	%	47.0	11.8	23.5	7.0	2.4	8.2	

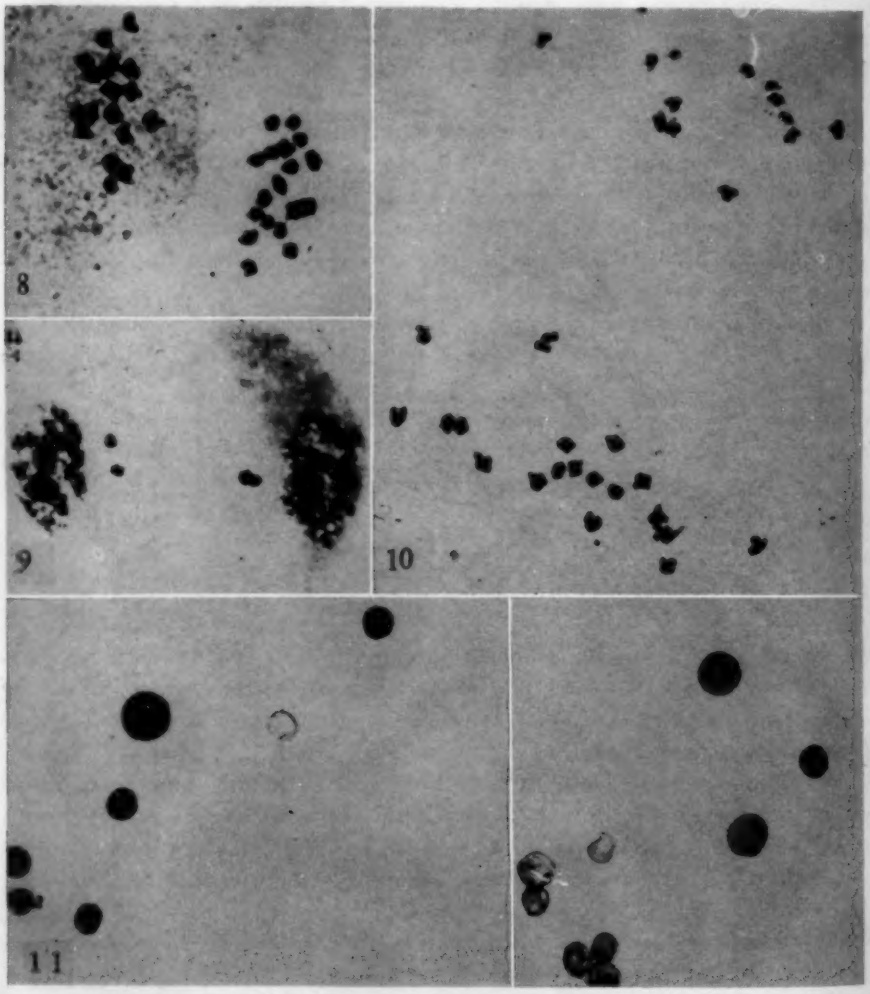
18:18; 18:17 with one lagging chromosome; 17:19; 17:17 with two lagging chromosomes, and 16:18 with two lagging chromosomes. The four entries had a similar frequency for these types as shown in Table 3. Other types were very infrequent.

By combining the data of the three entries it was found (from 85 cells) that 18:18 distribution occurred in 47.0% of the divisions (figs. 7 and 8) unequal distribution in 11.8% (fig. 10) and lagging chromosomes in 32.9%. The percentages of these different categories is given in Table 3.

From this it can be assumed that approximately 10–15% of the apparently normal daughter cells will be genetically unbalanced because of duplication and deficiency due to non-disjunction.

The totals from the four entries show that approximately 58% of the cells display abnormalities of one type or another (43% have lagging chromosomes, 3% have bridge + fragment, and 12% have unequal distribution of the chromosomes). If all of these factors are sufficient to cause sterility it would be expected that no more than 42% of the gametes produced would be viable.

At the dyad spore stage micronuclei were found in a high frequency of the cells (fig. 9) in the three entries studied. All entries were rather similar in regard to number and frequency of the micronuclei and the results are given in Table 4. From the combined figures of the three



FIGS. 8–10. Meiosis in *A. distachyus*. 1350×. FIG. 8. Anaphase I with normal 18:18 distribution of chromosomes. FIG. 9. Dyad spore stage with three micronuclei. FIG. 10. Anaphase I showing unequal distribution of the chromosomes, 19 to one pole and 17 to the other (part of this pole not included). FIG. 11. Pollen grain in A-5422 from Morocco (150×) showing large and small as well as dark, light, and empty grains.

entries 38.7% of the dyads were without micronuclei, 27.5% had one, 20.0% two, 6.3% three, 5.6% four, 0.6% five and 1.3% six.

TABLE 4. *Micronuclei at the dyad spore stage*

A-No.		Total Number	0	1	2	3	4	5	6
2644		52	15	15	12	4	5	1	0
3183		58	24	11	15	3	3	0	2
5422		50	23	18	5	3	1	0	0
Total	No.	160	62	44	32	10	9	1	2
	%		38.7	27.5	20.0	6.3	5.6	0.6	1.3

The second division was studied at anaphase and telophase in 78 cells of A-2644. Bridges were found occasionally (2.6%) and lagging chromosomes were seen in 9% of the cells. In no instances were these laggards dividing and it appears likely that they are the result of the divided univalents at the first division that were included in the daughter cells.

The few cells in which bridges were found at AII or TII were always without fragments and may have been the result of a double cross-over in a paracentric inversion in which one cross-over was outside the inverted region and the other within, or some similarly complex behavior. It may also have resulted from stickiness.

At the tetrad spore stage in the two entries studied 64.4% of the tetrads were without micronuclei and the others had various numbers ranging from one to seven. One was rather frequent (15.3%) whereas the other numbers were uncommon (Table 5).

TABLE 5. *Lagging chromosomes in second division and micronuclei at tetrad stage*

A-No.	Total No. Cells	Bridges No.	Bridges %	Laggers Frag.	Laggers No. Cells	Laggers %	Total Tetrads	Micronuclei 0	1	2	3	4	7
2644	78	2	2.6	0	7	10	29	16	7	2	1	2	1
5422	—	—	—	—	—	—	30	22	2	4	1	1	0
Total	—	—	—	—	—	—	59	38	9	6	2	3	1

Pollen fertility, as indicated by size and stainability in acetocarmine, was determined for one entry, A-5422. Anthers were dissected from the flowers some 24–48 hours before normal dehiscence. Four types of pollen grains were easily distinguishable by using size and color (fig. 11). Dark staining pollen grains were found in 28.9% of the cases but only 7.8% of these were large in size. Of the 71.1% light stained grains most were small (67.5%). Therefore it appears more than likely that no more than 29–30% of the pollen would be viable and possibly much less.

From the previous discussion of the cytological irregularities it was seen that only 58% of the cells had detectable irregularities, and 40% of the gametes would be expected to be viable. This 10% deviation from

the observed may be due to sampling error but may also be the result of genetic unbalance that is not obvious in a cytological study.

Discussion and conclusions. On the basis of the present study it appears that *Andropogon distachyus* L. has a basic number of nine with 2n = 36, and that the previous report of 2n = 40 for *A. distachyum* L. (Saura 1943) either referred to another species or that both x = 9 and x = 10 are present in the species. The first condition seems most likely to the author. Thus *A. distachyus* represents the first species of the genus *Andropogon* known to deviate from x = 10.

The meiotic behavior of the genus *Andropogon* is not well known but fifteen species have been studied by the author (unpublished). Nine of these were diploids (n = 10). In the diploids the chromosomes were always associated as bivalents, and in the six polyploids this was the most common condition. However, two of the polyploid species did occasionally have a quadrivalent but in no cell was more than one observed. In this respect *A. distachyus* is also quite unique since it has a high frequency of quadrivalents with as many as six being found in one cell. Not only is the frequency of multivalents greater than in other members of the genus *Andropogon* but it is only exceeded in the entire tribe by *Sorghum leiocladum, S. australiense,* and *S. plumosum* (Garber 1954). It was concluded by Garber (1954) that these *Sorghum* species are autopolyploids. When based on cytological evidence alone it is virtually impossible to separate autopolyploids from segmental allopolyploids as the terms are defined by Stebbins (1947, 1950), and no definite decision is being made at this time regarding *A. distachyus.*

The chromosomes of *A. distachyus* are rather large as compared with most other members of the Andropogoneae and compare favorably with the large chromosome genera *Sorghum* (Garber 1950), and *Elyonurus* (Brown 1951). By using comparative stages of metaphase I to those reported on for *A. distachyus,* seven other species of *Andropogon* were studied. Both diploids and polyploids were included. There were some differences between species but their averages ranged from 3.0 to 4.2 microns, all being much smaller than the 5.6 microns found for *A. distachyus.*

Morphologically the section *Eu-Andropogon,* which includes *A. distachyus,* is rather distinct from the other sections of *Andropogon.* According to Stapf (1919) the four sections of *Andropogon* may all deserve generic rank. Stapf (1919) reports that the section *Eu-Andropogon* contains about 12 species of Old World affinities and he lists 11 as being native of tropical Africa. With the exception of *A. distachyus* none of these have been studied cytologically.

From the cytological and morphological evidence it appears that *A.*

distachyus and possibly the section *Eu-Andropogon* are distinct from the bulk of the genus *Andropogon*. The extent to which this cytological distinctiveness of *A. distachyus* is representative of the *Eu-Andropogon* is not known and cytological information, including chromosome number, size, and meiotic behavior, is greatly needed.

SUMMARY

1. Four entries of *Andropogon distachyus* from Mediterranean Africa and Israel were studied cytologically.

2. All had 36 somatic chromosomes, with a basic number of 9. This is the first report of a basic number other than ten for *Andropogon*.

3. At diakinesis and metaphase I a large number of quadrivalents were found. From the number and frequency of these it was concluded that the species was either an autopolyploid or a segmental allopolyploid.

4. The chromosomes were much larger at metaphase I than in other species of the genus *Andropogon*.

5. Besides quadrivalents; univalents, bivalents, and trivalents were found at diakinesis and metaphase I, and lagging chromosomes, bridge + fragments, and non-disjunction were seen at anaphase and telophase I.

6. Micronuclei were found at both the dyad and tetrad spore stages, and lagging chromosomes and occasional bridges were seen at anaphase II.

7. Pollen fertility was found to be very low as expected from the cytological irregularities encountered.

8. The possible significance of these cytological conditions and the morphologically distinct *Eu-Andropogon* are discussed.

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Oklahoma A & M College

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THREE NEW NORTH AMERICAN VARIETIES OF KOBRESIA

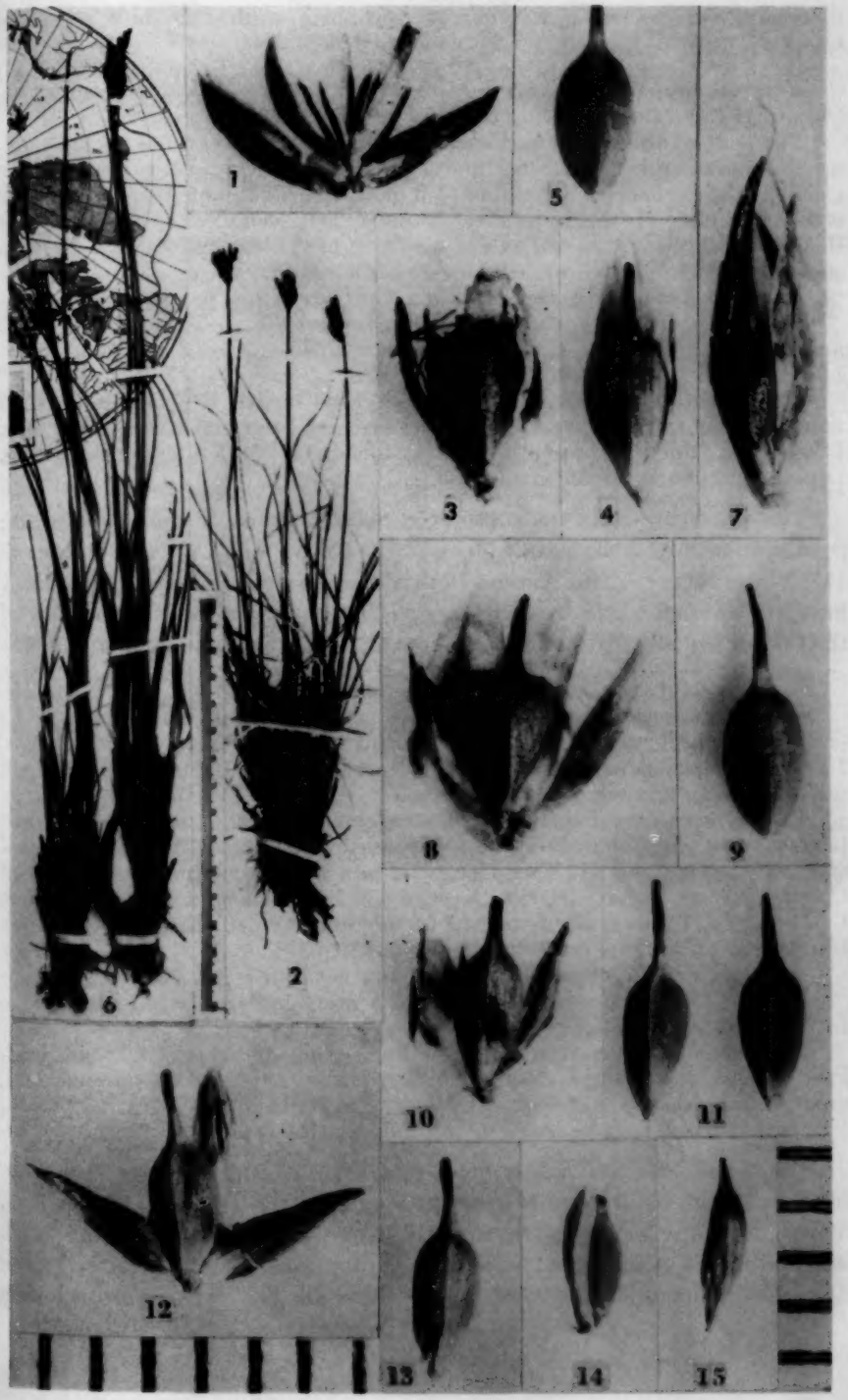
MAXIMILIAN G. DUMAN

The original material of *Kobresia macrocarpa* Clokey was distributed by Clokey as an undescribed *Elyna*. Mackenzie (1931) included the original description, which is obviously his own, in the North American Flora, but gave credit as the author of the new species to Clokey. It seems evident from the context that he considered the lateral spikelets pistillate, and the statement "the terminal flowers staminate, the lateral pistillate" probably refers to this condition. However, the lateral spikelets are androgynous, not only in the type material (Clokey 3651) but in the other Colorado material examined as well (Clokey 3317, Cox 444 and 406).

When Porsild (1943) published the original description of *Kobresia hyperborea* he observed that it "is perhaps most closely related to *K. macrocarpa* Clokey, of alpine peaks of Colorado, which, however, is well marked from ours in having 'the terminal flowers staminate and the lateral pistillate' and by having leaves that equal or exceed the culm." Actually both have androgynous lateral spikelets, and are very closely related. Each of these species has sterile scales inside the perigynium. In a similar species, *K. schoenoides* (C. A. Mey.) Steud. of Eastern Asia, we find three scales each bearing three stamens (staminate florets; fig. 1.). Rarely in *K. hyperborea* lower spikelets contain 2 staminate florets. In these the second is merely a simple scale bearing stamens. Hence I am referring to the scales which do not bear stamens as "sterile scales" to distinguish them from the staminate florets and the outer scales or glumes. I interpret these sterile scales as reduced staminate florets.

Alaskan material received from Ernest Lepage seems to differ sufficiently

FIG. 1. *Kobresia schoenoides*. Opened lateral spikelet showing 3 staminate florets and inconspicuous immature pistillate floret. Nilson 27-VI-1898. FIG. 2. *K. hyperborea* var. *hyperborea*. Porsild 2318 (Type). FIG. 3. Same Lateral spikelet, perigynium turned back to right; staminate floret and 2 sterile scales. FIG. 4. Same. Lateral spikelet. FIG. 5. Same. Achene. FIG. 6. *K. hyperborea* var. *alaskana*. Lepage and Murie 25538 (Type). FIG. 7. Same. Lateral spikelet with achene, 2 sterile scales and staminate floret enclosed by the perigynium. FIG. 8. Same. Lateral spikelet opened; perigynium (rear, left), 3 sterile scales, and staminate floret (right). FIG. 9. Same. Achene. FIG. 10. *K. hyperborea* var. *lepagei*. Lateral spikelet opened; perigynium (left), staminate floret (right) and 1 sterile scale. Lepage 23640 (Type). FIG. 11. Same. 2 achenes. FIG. 12. *K. macrocarpa*. Lateral spikelet with perigynium removed; 2 sterile scales and staminate floret (rear, right). Clokey 3317. FIG. 13. Same. Achene. FIG. 14. *K. simpliciuscula* var. *americana*. Achene and long rachilla with scale-like end. Dutilly, Lepage and Duman 28118. FIG. 15, *K. simpliciuscula* var. *simpliciuscula*. Achene and rudimentary rachilla. Zellersted and Wickbon, Norway. Figures 2 and 6, reduction as shown in figure 2. Other figures, magnification as shown by mm scale at bottom of plate.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to receive varietal rank. For comparison some additional data are given for the typical variety.

Kobresia hyperborea var. *hyperborea*. (figs. 2, 3, 4, 5.; Description, Porsild 1943; Name and illustration, Porsild 1951).

The ends of the leaves curl giving an unkempt appearance to the specimens; lateral spikelets 4.5–5.5 mm long, 1.8 mm wide, containing 2 or 3 sterile scales; achenes 2.8 mm long, 1.5 mm wide. The photograph in figure 2 is of a specimen on the Type sheet, Porsild 2318. Another specimen on this sheet is taller, nearly as tall as the specimen of *K. hyperborea* var. *alaskana* shown in figure 6, but most of its leaves are missing.

Kobresia hyperborea var. **alaskana** var. nov. (figs. 6, 7, 8, 9.).

Foliis rectioribus; spiculis lateralibus majoribus, 6–7 mm longis, 1.8–2 mm latis, cum 3, raro 2, squamis sterilibus; nuculis 2.6–2.8 mm longis, 1.5–1.7 mm latis.

The leaves are straighter; lateral spikelets larger, 6–7 mm long, 1.8–2 mm wide, containing 3, rarely 2, sterile scales; achenes 2.6–2.8 mm long, 1.5–1.7 mm wide. Peaty place along Savage River, McKinley Park, Alaska. Lepage and Murie 25538 (Holotype, LCU; Isotype, LAT.

Two immature collections also from Alaska probably also belong here; Spetzman 2526A, Alaska Half Moon 3, 70° 45′ N.; 155° W., and Gjaerevall 147, White Mts., Central Alaska. Both of these are very immature, but they have the characteristic straight leaves. The immature lateral spikelets of the former are already 5 mm long, those of the latter are too immature to be significant.

Kobresia hyperborea var. **lepagei** var. nov. (figs. 10, 11.).

Planta tenuior, foliis rectioribus; spiculis lateralibus 4.2–5.2 mm longis, 1.3 mm latis, cum unica squama sterili (rarissime 2 in spiculis infimis); nuculis 2.6–2.8 mm longis, 1.2 mm latis.

The plant is more delicate, leaves straighter; lateral spikelets 4.2–5.2 mm long, 1.3 mm wide, containing only one sterile scale (very rarely 2 in lowest spikelets); achenes 2.6–2.8 mm long, 1.2 mm wide. Dry ridge north side of Colville River, Umiat, Alaska. Lepage 23640 (Holotype, LCU; Isotypes, CAN, LAT). This variety is named for my good friend, Ernest Lepage, my companion on various northern rivers and trails.

Kobresia simpliciuscula var. **americana** var. nov. (fig. 14.).

A typo differt nuculis brevioribus, 2.5 mm longis, et stipitatis squamiformibusque rachillis longis.

This variety differs from the type by its shorter achenes, 2.5 mm long, and its long, scale-like stalked rachillae. Grassy shelf of magnesian rock, mountain on west side of Koksoak River, 2 miles below the fork, 57° 42′ N., Ungava. Dutilly, Lepage and Duman 28118 (Holotype, LCU).

The type locality of *K. simpliciuscula* (Wahl.) Mackenize is Westmoreland, England. Most authors give the length of the achene as 3 mm long. This is too long for our North American material. North American specimens also have long, stalked scale-like rachillae, nearly as long as the achene (fig. 14.). Kükenthal (1909) stated, "Rachilla . . . brevis stipitiformis

saepe adest." Mackenzie (1931) wrote, "Rachilla sometimes present, short, very slender." These statements are correct for European (fig. 15.) and Greenland specimens, but they certainly do not apply to our North American plants.

SUMMARY

1. *Kobresia schoenoides* (C. A. Mey.) Steud. of Eastern Asia has androgynous lateral spikelets containing 3 stameniferous scales.

2. *K. macrocarpa* Clokey of Colorado and *K. hyperborea* Porsild of northwestern Canada have androgynous lateral spikelets containing 2 or 3 sterile scales inside the perigynia.

3. *K. hyperborea* var. *alaskana* var. nov. of Alaska has straighter leaves and larger lateral spikelets containing 2 or 3 sterile scales.

4. *K. hyperborea* var. *lepagei* var. nov. of Alaska has straighter leaves and narrower lateral spikelets with only 1 sterile scale.

5. *K. simpliciuscula* var. *americana* var. nov. of North America differs from the typical variety of Europe and Greenland by its shorter achenes and its long, scale-like stalked rachillae.

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PRODUCTION OF ZOOSPORES FROM GERMINATING OOSPORES OF PYTHIUM MAMILLATUM MEURS

CHARLES DRECHSLER[1]

In an earlier paper (Drechsler 1952) I described the production of swarm spores from germinating oospores of *Pythium ultimum* Trow and *P. debaryanum* Hesse, two fungi widely familiar as parasites causing damping-off, root rot, and stem rot in many crop plants. Such germinative development has since been observed also in *P. mamillatum* Meurs (1928), a fungus of rather similar pathogenic character, which from its morphological resemblances to *P. debaryanum* must be considered a close relative of that species. These resemblances, however, might easily escape attention, for owing to the presence of many protuberances on its oogonia, *P. mamillatum* presents a bristling appearance strongly suggestive of such less intimately related spinose congeners as my *P. acanthicum* and my *P. anandrum*. To show the usual variations in the fungus held referable to Meurs' species, units of asexual and sexual reproductive apparatus selected largely at random in maize-meal agar plate cultures of two isolations are herein figured in numbers sufficient, it is hoped, to make up tolerably representative assortments. One of the isolations (figs. 1 and 2) was obtained early in August, 1926, from a discolored rootlet of a tomato (*Lycopersicon esculentum* Mill.) plant removed from a field in Arlington, Virginia. The other (figs. 3 to 5) came from a discolored rootlet of a sheep sorrel (*Rumex acetosella* L.) plant dug up near Beltsville, Maryland, on April 29, 1949. Both isolations correspond well to a culture of *P. mamillatum* contributed by Meurs to the Centraalbureau voor Schimmelcultures at Baarn, Netherlands, and now being maintained also in the American Type Culture Collection, Washington, D. C., under the designation ATCC11121.

A mycelium of *Pythium mamillatum* actively growing in a Petri plate of

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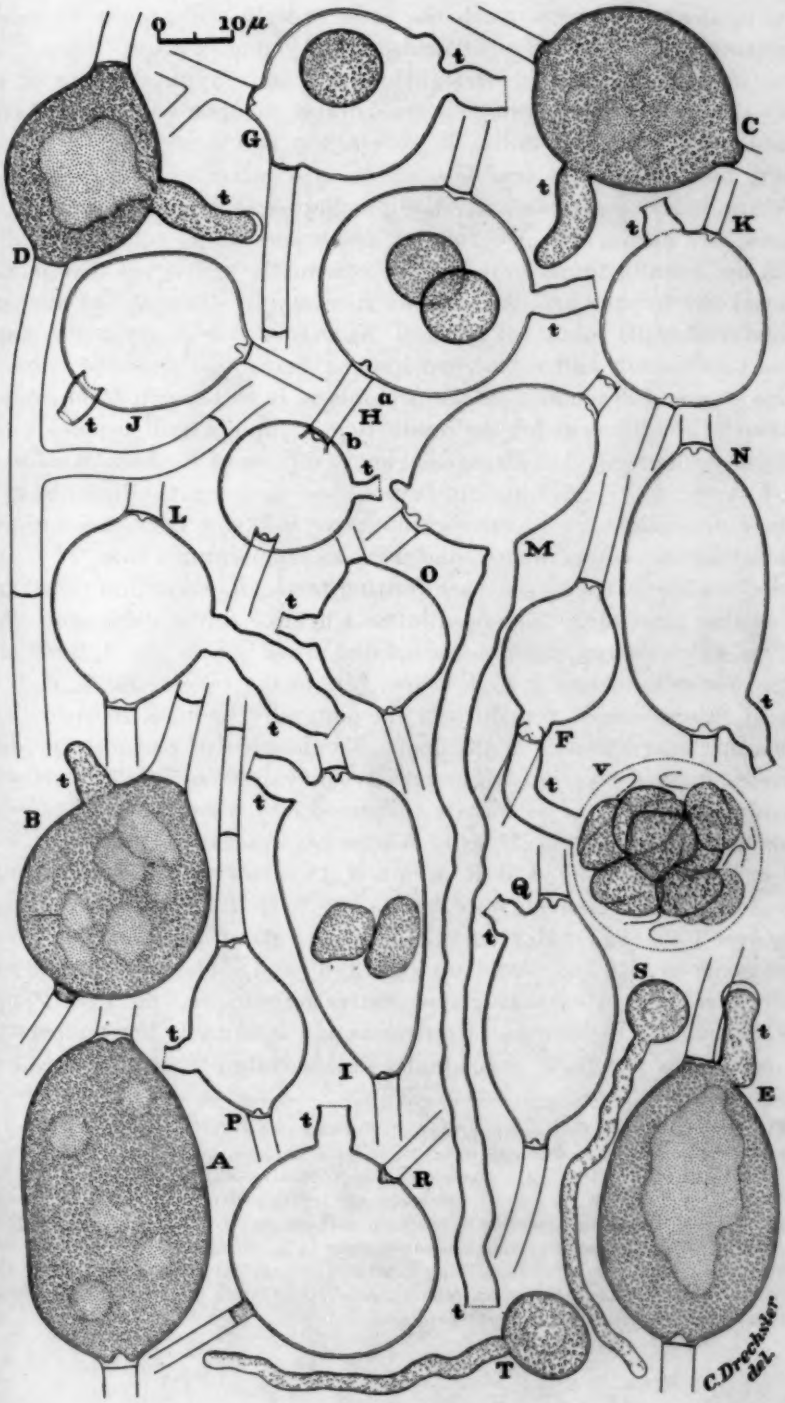
FIG. 1. Asexual reproductive apparatus of *Pythium mamillatum* (tomato strain) produced on irrigated slabs excised from a maize-meal agar plate culture; drawn at a uniform magnification with the aid of a camera lucida; ×1000. A. Large sporangium. B, C. Two sporangia, each putting forth an evacuation tube, t. D, E. Two sporangia ready to discharge their contents, each bearing an evacuation tube, t, with a hyaline cap of dehiscense. F. Sporangium showing empty evacuation tube, t, and vesicle, v, containing 8 motile zoospores. G, H (a, b), I–R. Sporangia after conversion of their contents into swarm spores; t, empty evacuation tube. S, T. Encysted zoospores, each with a vegetative germ tube.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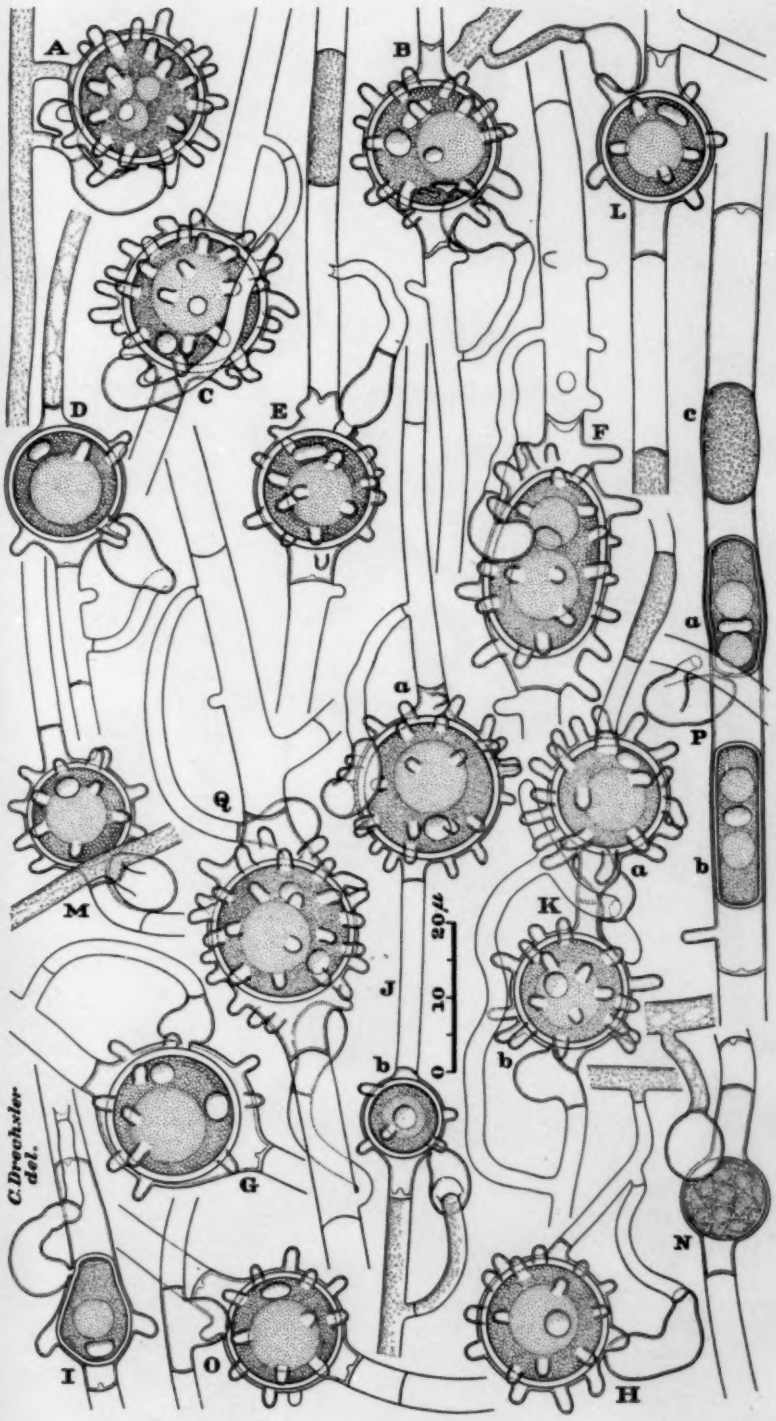
maize-meal agar presents much the same orderly appearance whereby *P. debaryanum* may often be distinguished, in young cultures, from *P. ultimum;* its radially oriented, straightforward, main hyphae giving off relatively short, irregularly ramified branches at moderate intervals. Like *P. debaryanum*, again, but unlike *P. acanthicum* and most other spinose congeners, the fungus in a few days produces a rather copious white aerial mycelium, which later often gradually collapses in large areas of the substratum as a fibrous mat. The tubular membranes of the empty matted filaments are usually found only rather indistinctly visible, so that in much material the hyphae are disclosed to view mainly through the numerous convex cross-walls contained in them. Numerous convex septa also appear in the procumbent and submerged hyphae, being laid down to mark successive stages of evacuation as the protoplasm is withdrawn from extensive portions of the filament for the production of conidia and oospores.

The conidia formed in maize-meal agar cultures of *Pythium mamillatum* (fig. 1, A; fig. 3, A) differ little in their globose or elongate-ellipsoidal shape, in their dimensions, or in their germinative behavior from the conidia of *P. debaryanum*. Under moist conditions at temperatures near 17°C. they develop readily as sporangia, each putting forth an evacuation tube (fig. 1, B-C:t) that after some elongation forms a hyaline cap of dehiscense (fig. 1, D–E: t) which on yielding becomes inflated into a vesicle (fig. 3, B, v) as the protoplasm streams into it from below. Within the vesicle (fig. 1, F, v) the mass of protoplasm is transformed into laterally biciliate zoospores after the manner characteristic of the genus. The number of zoospores produced from sporangia of mycelial origin varies commonly from 5 to 30. Portions of protoplasm that fail to escape are fashioned into zoospores inside the sporangial envelope (fig. 1, G; H, a; I). The empty evacuation tube (fig. 1, F–G: t; H, a–b: t; I–R: t; fig. 3, B–R: t, S, a–b: t) varies considerably in length, in some instances measuring only 2 or 3μ (fig. 3, Q–R: t) and in others measuring over 100μ (fig. 1, M, t). After swimming about for some time the zoospores come to rest and round up (fig. 3, T, a–n). The subspherical cysts usually germinate by extending a vegetative germ hypha (fig. 1, S, T; fig. 3, U–W), though in the absence of nutrients and at suitably low temperatures they sometimes put forth individually an evacuation tube (fig. 3, X) and

FIG. 2. Sexual reproductive apparatus of *Pythium mamillatum* (tomato strain) produced in maize-meal agar plate cultures; drawn at a uniform magnification with the aid of a camera lucida; ×1000. A. Monoclinous reproductive unit with oospore somewhat immature. B–I, J (a, b), K (a, b). Monoclinous reproductive units, each with mature oospore and with oogonium attended by a single antheridium. L–P. Diclinous reproductive units, each with single antheridium; oospore mature in L, M, and O, but immature in N; the cylindrical oogonium of P containing 2 mature cylindrical oospores, a and b, and a vegetative segment or conidium, c. Q. Monoclinous reproductive unit with mature oospore and with oogonium attended by 2 antheridia.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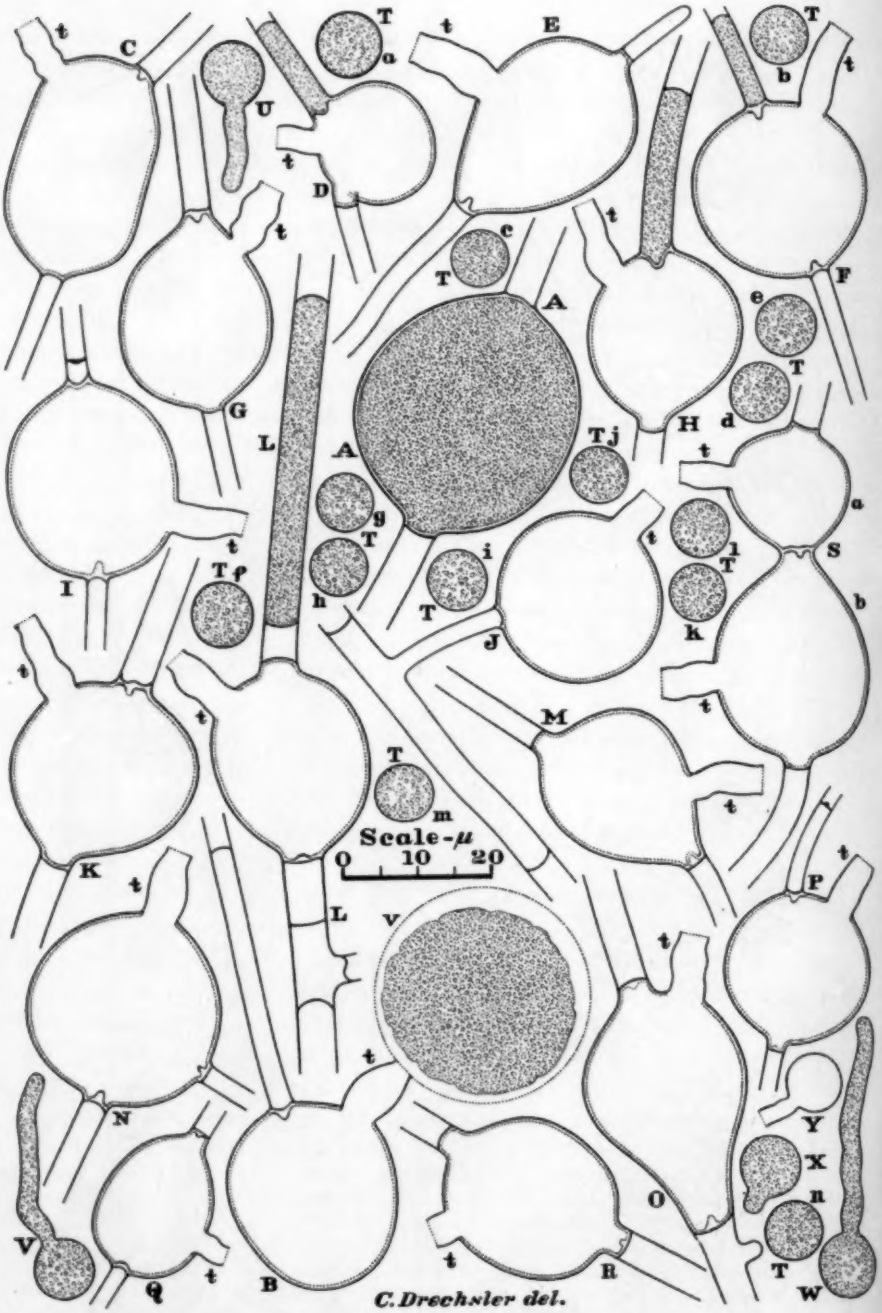

FIG. 3. *Pythium mamillatum* (sheep sorrel strain), × 1000. A. Large sporangium. B. Newly emptied sporangium; t, evacuation tube; v, vesicle. C–R, S (a, b). Empty sporangia; t, evacuation tube. T. Encysted zoospores, a–n. U–W. Encysted zoospores germinating vegetatively. X. Zoospore cyst with short evacuation tube. Y. Zoospore cyst after escape of protoplast.

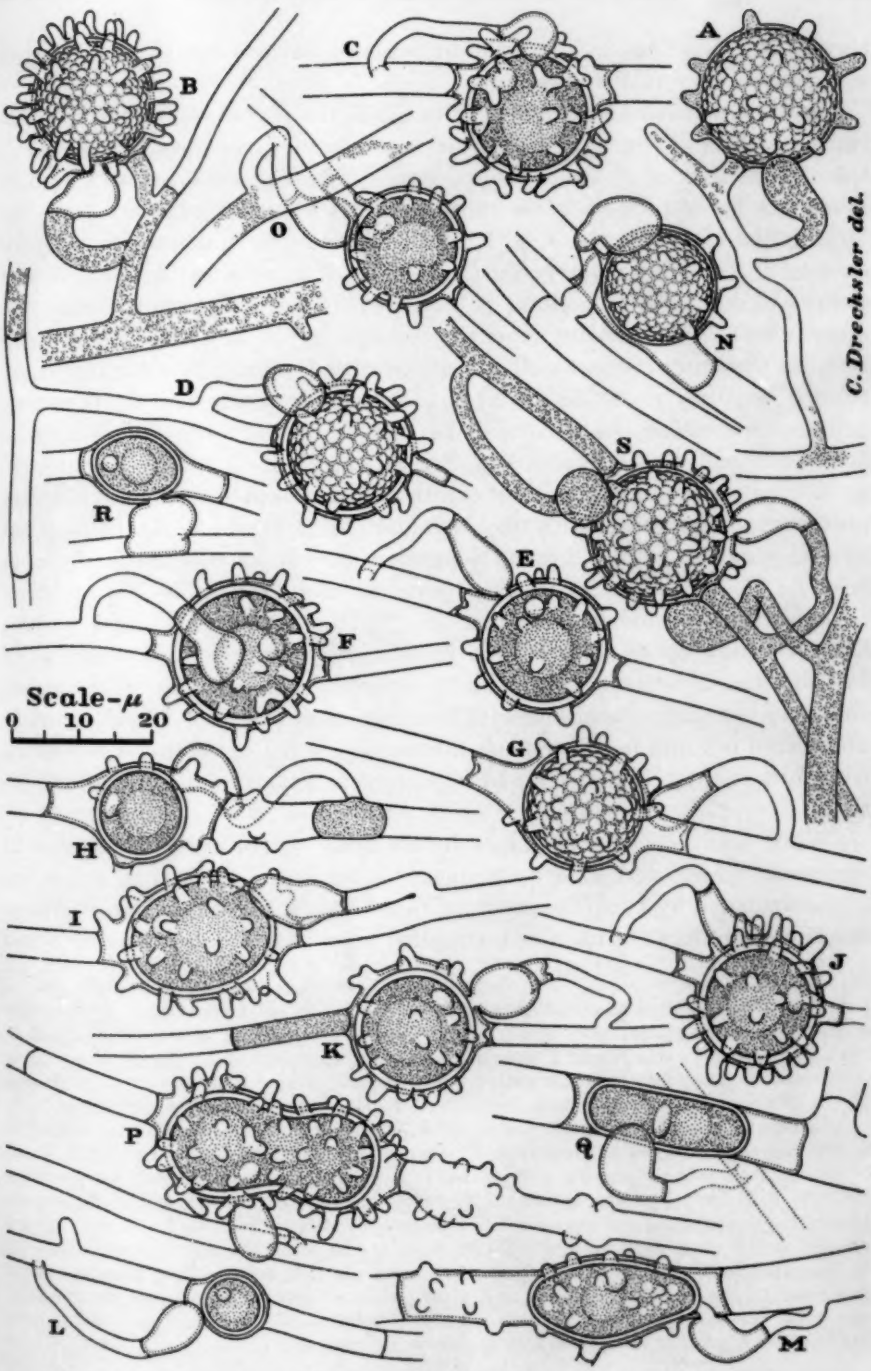

FIG. 4. Sexual reproductive apparatus of *Pythium mamillatum* (sheep sorrel strain), ×1000. A–M. Monoclinous units with single antheridia. N–R. Diclinous units with single antheridia. S. Unit with 3 antheridia.

become emptied (fig. 3, Y) as the protoplasm streams out to be converted into a secondary motile zoospore.

In the positional arrangement of its parts the sexual reproductive apparatus (fig. 2, A–Q; fig. 4, A–S) of *Pythium mamillatum* shows general parallelism with that of *P. debaryanum*. Sometimes the oogonium and antheridium are borne terminally on short branches arising separately from the same hypha (fig. 2, A; fig. 4, A, B). Much more often in monoclinous reproductive units an intercalary (fig. 2, B–G; I; J, a, b; K, a; fig. 4, C–M) or terminal (fig. 2, H) oogonium is fertilized by an antheridium borne terminally on a branch arising from the oogonial hypha at a distance of 5–40μ from the oogonium. Occasionally an oogonium is fertilized by an antheridium formed adjacent to it (fig. 2, K, b). Diclinous reproductive units appear neither exceptional nor abnormal. In such units the antheridium may be borne terminally on a branch (fig. 2, L–N; fig. 4, N–Q), or may consist of an intercalary portion of hypha together with a somewhat massive lateral protuberance in contact with the oogonium (fig. 2, O; fig. 4, R). Cylindrical hyphal segments which develop somewhat tardily as oogonia in forming one (fig. 4, Q) or two cylindrical oospores (fig. 2, P, a, b), in addition, perhaps, to a cylindrical conidium (fig. 2, P, c), are often found to have been fertilized by an antheridium from a neighboring hypha. Oogonia of such belated development are usually altogether smooth (fig. 4, Q) or are only very sparingly furnished with protuberances (fig. 2, P). Pronouncedly undersized oogonia in either monoclinous (fig. 4, L) or diclinous reproductive units (fig. 2, N; fig. 4, R) likewise appear usually devoid of protuberances.

While many oogonia produced by *Pythium mamillatum* in maize-meal agar cultures are fertilized by a single antheridium, more than a few are found attended by two (fig. 2, Q) or three (fig. 4, S) antheridia. With respect to the number of male cells supplied to an oogonium the fungus would

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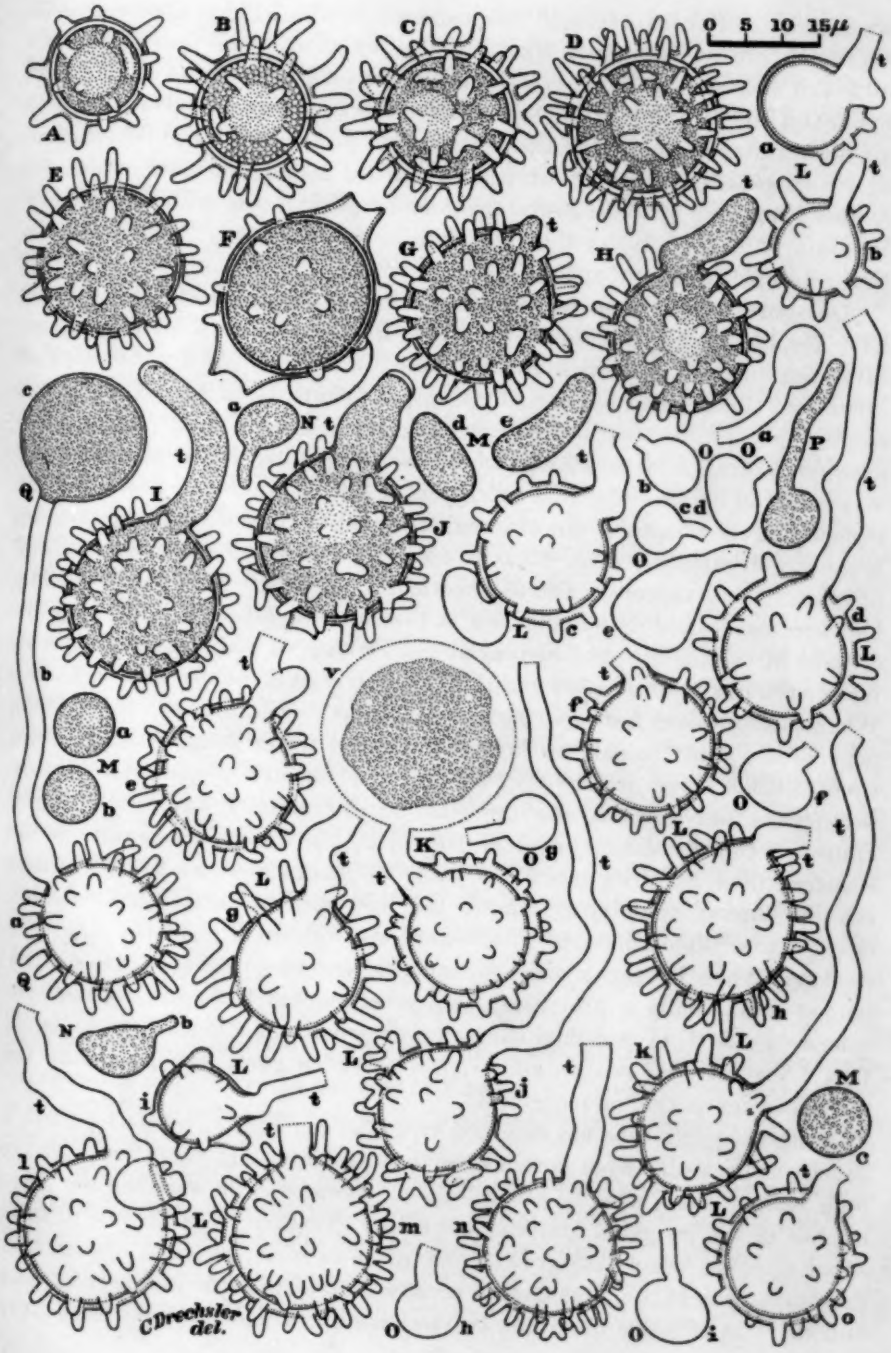
FIG. 5. Germination of oospores taken from 60-day-old maize-meal agar plate culture of *Pythium mamillatum* (sheep sorrel strain); parts A–D showing specimens as found in the aging culture, parts E and F showing specimens after irrigation for 24 hours, parts G–Q showing specimens after irrigation for 48 hours; drawn with the aid of a camera lucida at a uniform magnification; ×1000. A, B. Oospores with single refringent body. C, D. Oospores with 2 refringent bodies. E, F. Oospores in which the wall is reduced in thickness and surrounds a protoplast of coarsely granular texture throughout. G, H. Oospores, each with a growing germ tube, t. I, J. Oospores nearly ready to discharge contents, each having an evacuation tube, t, with a hyaline cap of dehiscense. K. Oospore soon after discharging its contents; t, evacuation tube; v, vesicle. L. Empty oospore envelopes, a–o, each with open evacuation tube, t, extending through the oogonial wall. M. Encysted zoospores, a–e. N. Encysted zoospores, a and b, each bearing a short evacuation tube. O. Empty zoospore cysts, a–i, after escape of protoplast through open evacuation tube. P. Encysted zoospore with vegetative germ tube. Q. Empty oospore, a, with empty germ hypha, b, terminating in a globose sporangium, c.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thus seem to differ little from *P. debaryanum,* in which I have observed no instances where an oogonium was attended by more than four antheridia although Matthews (1931), as also Middleton (1943), includes among some first-hand illustrations of Hesse's species a sexual reproductive unit with six antheridia, all applied to the oogonium in profile view. The illustrations of *P. mamillatum* given by Matthews and by Middleton show more pronounced tapering of the oogonial protuberances than was evident in Meurs' isolation (ATCC11121) or than would seem present in any American isolation referable to Meurs' species.

Ooospores of *Pythium mamillatum* formed in maize-meal agar cultures have for the most part shown relatively little reorganization of contents after the cultures had been stacked under a battery jar for 60 days at laboratory temperatures near 20°C. Some among them would then still retain the internal structure characteristic of the resting state (fig. 5, A),—each containing a large homogeneous reserve globule, a parietal granular layer, and an oblate ellipsoidal refringent body. In others the parietal layer seemed largely composed, not of irregular granules, but of rounded particles arranged circularly (fig. 5, B) as in resting oospores of *Aphanomyces* and of some related saprolegniaceous genera. In still others the reserve globule had become noticeably smaller, while the parietal layer had not only increased in volume but now displayed two refringent bodies as well as scattered vacuolar inclusions of rounded or of irregular shape (fig. 5, C, D). When such oospores were sparingly irrigated in Petri dishes at temperatures near 17°C., with the shallow layer of distilled water being changed from time to time, they acquired in 24 hours a uniformly granular texture throughout the interior, and the wall became thinner and more tightly appressed to the oogonial envelope (fig. 5, E, F). Under wet conditions the oospores thus acquired much the same appearance as asexually formed conidia, having undergone during the first day of irrigation the same changes that the oospores of *P. ultimum* undergo directly in the stale substratum. When irrigation was continued a second day many oospores extended individually a protrusion that soon erupted from the oogonial envelope (fig. 5, G, t) and then elongated externally as a germ hypha (fig. 5, H, t). Virtually all remaining oospores extended germ hyphae during the third 24-hour period of irrigation.

Once the germ tube has emerged from the oogonial envelope its further development would seem governed mainly by environal conditions. At the high temperatures usually prevailing in laboratories in summer the germ hyphae in my irrigated material commonly grew out vegetatively to form small mycelia. Vegetative growth took place in some instances also at temperatures near 17°C., presumably because nutrients were still present here and there in effective quantity. In most instances, however, at these lower

temperatures the germ hypha ceased to elongate and formed a hyaline cap of dehiscense (fig. 5, I–J : t). This cap became inflated into a vesicle (fig. 5, K, v) in which the undifferentiated protoplasm discharged from the oospore was converted into motile swarm spores. The empty membranous envelopes showed variations in the lengths of evacuation tubes (fig. 5, K, t; L, a–o : t) similar to the variations in lengths of evacuation tubes on sporangia of mycelial origin. The empty oospore wall appeared of equal or slightly greater thickness than the oogonial envelope, from which it was only rather slightly separated in some instances (fig. 5, L, h, n), and more widely in other instances (fig. 5, L, d, o).

The zoospores produced from germinating oospores in numbers varying usually from 4 to 12, like those produced generally in somewhat greater number from ordinary sporangia, commonly measured 7.5 to 10μ in diameter after they had rounded up (fig. 5, M, a–c). Oversized elongated zoospores (fig. 5, M, d, e) were observed mainly in portions of irrigated material not adequately supplied with water for complete cleavage. Some encysted zoospores soon extended a short evacuation tube (fig. 5, N, a, b) and became emptied (fig. 5, O, a–i) by discharging their contents to be transformed into secondary motile zoospores. Others pushed out individually a vegetative germ hypha (fig. 5, P) capable of growing into a mycelium.

Some oospores of *Pythium mamillatum* (fig. 5, Q, a) germinated by putting forth a germ hypha (fig. 5, Q, b) that soon ceased to elongate and thereupon gave rise to a terminal conidium or sporangium (fig. 5, Q, c). Such germination took place at midsummer temperatures as well as at lower temperatures suitable for development of swarm spores. Sporangia produced externally by oospores without intervention of a vegetative stage commonly yield 4 to 12 swarm spores. Their progenies, as might be expected, are approximately equal to the progenies of oospores that become directly converted into sporangia, and accordingly are less numerous than the progenies issuing from the larger of the sporangia formed asexually on well nourished mycelium.

SUMMARY

1. *Pythium mamillatum* appears intimately related to *P. debaryanum* as it resembles that species in the branching habit of its mycelium, in the shape and size of its sporangia, and in the positional relationships of its oogonia and antheridia.

2. A germinating oospore of *Pythium mamillatum* may produce swarm spores by undergoing conversion into a sporangium, or by giving rise to a globose sporangium outside the oogonial envelope.

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COMPOSITION OF PRE-SETTLEMENT FORESTS IN THREE COUNTIES OF MISSOURI

D. L. HOWELL AND C. L. KUCERA

The influence of civilized man on primeval American vegetation has produced significant changes over extensive areas. Because of continuing modification and depletion, examples of undisturbed, native vegetation are becoming increasingly less available for study and observation. Early investigators usually had sufficient stands for determining general distributions on a regional basis. A problem of a more local nature, as well as perhaps a more difficult one, is raised in analyzing the zone of transition between formations when changes in the original vegetation have occurred.

The purpose of this study was to reconstruct, from the early territorial survey data, the pre-settlement forest cover of three Missouri Counties in the forest-prairie border. The disposition of this forest and the adjunct prairie, and regional trends in species importance are objectives of particular interest. The relationship between the forest-prairie transition and soil distributions as a possible indication of former shifts of vegetation also is considered.

The use of original survey information as a basis of determining plant distributions has been employed widely in the states of the East and Midwest. Studies have been conducted in New York (Gordon 1940), Pennsylvania (Lutz 1950), Ohio (Sears 1925), Indiana (Blewett and Potzger 1951; Potzger 1935; Potzger and Keller 1951; Potzger and Potzger 1950; Rohr and Potzger 1951), Michigan (Dick 1936; Kenoyer 1929; 1933–1939), Wisconsin, Ellarsan, 1949; Fassett, 1944), and Iowa (Dick-Peddie 1952). Sears (1921) who early tested the accuracy of witness tree identifications considered the method generally reliable. More recently a similar opinion was indicated by Potzger and Potzger (1950).

Investigations. In the present study a determination of forest composition at the time of the original land surveys was made for three Missouri Counties. These were Clark, Boone, and Dade Counties in northeastern, central, and southwestern sections of the state, located along the line of forest-prairie transition. Witness tree data and accompanying notes of the original territorial surveys provided information for the study. The mechanics of survey are well known and will not be reviewed here. Notes were transcribed and processed to indicate forest composition in each of the three counties. Tree size and density, by species, were evaluated and compared. Forest-prairie boundaries were drawn in by connecting a series of plots each of

which, according to information entered by the surveyor, marked the point on the section line where the transition zone occurred. The bearing or direction of the boundary being crossed was also indicated by the surveyor, which facilitated orientation of the transition line.

Terminology. In identifying witness trees in the three counties of the present study, the surveyors usually employed specific designations. Only five of the 4199 oaks recorded in the present study were listed simply as oak. Other groups were also indicated by specific common names including box-elder and sugar maple. Occasionally witness trees were identified only generically by terms such as hickory, elm, and ash.

Forest Composition and Distribution. Species recorded as witness trees are listed in Table 1 by total number of individuals and by percentage composition for each county and for the three counties combined. There were 35 different tree designations recorded in the original survey notes for Clark County, 38 for Boone County, and only 23 for Dade County, the latter in the southwestern portion of Missouri. For all counties, a total of 47 designations was tabulated.

Inspection of survey data shows that the forested areas of the three study areas were dominated by (*Quercus* spp.) at the time of the land surveys. The forest compositions of Clark and Boone Counties were generally similar. The Dade County forest, in the southwest portion of the state, however, appeared different from the other two. The oaks were proportionately of greater importance in the southwestern county, representing approximately 76 per cent of all witness trees. This figure compares with 66 per cent oaks in Clark County and only 58 per cent in Boone County. Differences occurred also regarding the geographic importance of the various species of *Quercus*. Two oak complexes became evident upon examination of data in Table 1. A northern one found in Clark and Boone Counties was characterized by *Q. alba* and *Q. macrocarpa*. These are two prominent species of the Central Hardwoods. The latter, as noted by Braun (1950) assumes greater prominence in the northern or glaciated portions of the region. Both counties occur within or on the boundaries of glaciation.

The data from Dade County in the western Ozarks of Missouri indicate a second oak complex in whiich *Q. stellata* and *Q. marilandica* predominate. These two species accounted for 66 per cent of all oak witness trees. This variable composition of forests across Missouri would reaffirm the view of Potzger and Keller (1951), who cautioned against the unqualified use of the term "oak-hickory" forest. The post oak-blackjack forests of Dade County apparently are associationally related to the disjunctive hardwood communities of Oklahoma and Texas. At these southwestern limits of the deciduous forest, *Q. stellata* and *Q. marilandica* are the principal tree species in a characteristically grassland climate. According to Dyksterhuis (1946)

TABLE 1. *Number of species and the witness tree composition by counties and on a total basis.*

Total number of species	Clark County 35		Boone County 38		Dade County 23		TOTAL 47	
	No.	%	No.	%	No.	%	No.	%
Quercus alba[1]	518	29.70	1292	39.00	42	2.86	1852	28.50
Q. macrocarpa	428	24.60	546	16.40	42	2.86	1016	16.92
Q. marilandica	5	0.29			258	17.60	263	4.05
Q. stellata	4	0.23	16	0.48	485	33.00	505	7.78
Q. velutina			6	0.18	208	14.20	214	3.30
Q. palustris	67	3.86	10	0.30	38	2.60	115	1.77
Q. rubra	71	4.08	66	1.98	13	0.89	150	2.31
Q. falcata	1	0.06			20	1.36	21	0.32
Q. bicolor			1	0.03			1	0.02
Q. imbricaria	38	2.18					38	0.58
Q. lyrata	17	0.98					17	0.26
Q. nigra					2	0.14	2	0.03
Quercus spp.					5	0.34	5	0.08
All oaks	1149	65.98	1937	58.37	1113	75.85	4199	64.60
Carya illinoensis	3	0.17					3	0.05
Carya spp.	155	8.98	328	9.90	283	19.30	766	11.79
Tilia americana	26	1.50	57	1.70	1	0.07	84	1.29
Acer saccharum	9	0.52	182	5.50			191	2.94
A. Negundo	4	0.23	21	0.63	2	0.14	27	0.42
Acer spp.	21	1.21	8	0.24	1	0.07	30	0.46
Fraxinus spp.	18	1.04	121	3.65			139	2.14
Fraxinus quadrangulata			7	0.21			7	0.11
F. americana			2	0.06			2	0.03
Ulmus alata			1	0.03			1	0.02
U. Rubra					1	0.07	1	0.02
Ulmus spp.	196	11.30	267	8.05	14	0.96	477	7.34
Juglans cinerea	2	0.12	2	0.06	1	0.07	5	0.08
J. nigra	15	0.87	4	0.12	7	0.48	26	0.40
Juglans spp.	8	0.46	82	2.46	21	1.43	111	1.71
Betula spp.	13	1.10	8	0.24			21	0.32
Salix spp.	4	0.23	2	0.06			6	0.09
Ostrya virginiana	1	0.06	18	0.54			19	0.29
Populus deltoides	36	2.07	27	0.81			63	0.97
Celtis occidentalis	24	1.38	118	3.56	2	0.14	144	2.20
Aesculus spp.	3	0.17	7	0.21			10	0.15
Gleditsia triacanthos	5	0.29	17	0.51			22	0.34
Prunus spp. (cherry)	12	0.70	3	0.09	2	0.14	17	0.26
Prunus spp. (plum)			1	0.03			1	0.02
Platanus occidentalis	6	0.35	38	1.14	12	0.82	56	0.86
Morus rubra	4	0.23	21	0.63	1	0.07	26	0.40
Crataegus spp.	1	0.06					1	0.02
Gymnocladus dioica	2	0.12	9	0.27			11	0.17
Juniperus virginiana	1	0.06	1	0.03			2	0.03
Cercis canadensis	2	0.12	4	0.12			6	0.09
Pyrus spp.	3	0.17	1	0.03			4	0.06
Sassafras albidum			5	0.15			5	0.08
Asimina triloba			3	0.09			3	0.05
Cornus spp.			14	0.42			14	0.22
Total	1723	100.	3316	100.	1461	100.	6500	100.

[1] Nomenclature follows Gray's Manual of Botany. ed. 8, 1950.

grasses constitute the climatic climax. The two oak species are regarded as the xerophytic remnants of a formerly broader extension of the eastern deciduous forest.

In the present study, other groups and species of witness trees in descending order of percentage importance were *Carya* spp., *Ulmus* spp. *Acer saccharum, Celtis occidentalis, Fraxinus* spp. *Juglans* spp., and *Tilia americana*. Both *Carya* spp. and *Ulmus* spp. were generally of equal importance in Clark and Boone Counties. In Dade County, however, hickory occurred in a ratio of approximately 19 to 1, to the elm species. The latter constituted about one per cent of the total witness tree tabulation for that county. Sugar maple designated as such was not recorded in the southwest study area, though present in the others.

The distance of witness trees from section and quarter section corners, recorded in the survey, was interpreted as a measure of relative forest density. Examination of distance data for all species indicated that Boone County was the most densely wooded of the three areas, and Dade County the least. The mean distance in feet (*converted from links as expressed in the survey*) from corner calculated from species means was Boone, 23.36 ± 4.24; Clark 49.17 ± 8.00; and Dade 61.71 ± 14.01. The greatest variation in distances is indicated for Dade County by the relative size of the standard error, and the least for Boone County. The largest witness trees including a 74 inch burr oak were recorded for Boone County. Two 60 inch white oaks were also listed. Mean diameters for all witness trees were 12.3, 12.6, and 13.2 inches for Boone, Clark, and Dade Counties, respectively. The large sizes of particular individuals found in Boone County together with the smallest average distance from section corners, and the largest number of species (Table 1) indicate possibly the oldest forest development of the three areas. These criteria, however, are not necessarily indicative as discussed by Cain (1944). On such bases alone, the inferred relationship of relative antiquity and frequency and abundance may be unreliable.

In order to ascertain relative abundance of tree species associated with prairies and barrens, all witness trees recorded in areas designated as such by the surveyor were treated together in each county.

Marked regional trends in prairie associates were indicated in the tabulations. In the northern portion of the transition of Missouri, including Clark and Boone Counties, *Quercus alba* and *Q. macrocarpa* were the principal species. The former diminished from 37.8 per cent of all witness trees in the prairie and barrens of Clark County to 6.0 per cent in the southwest, and the latter from 36.1 to 2.0 per cent. It was shown from survey data for eastern Iowa that *Quercus macrocarpa* also was an important forest species in the prairie ecotone (Dick-Peddie 1952). Studies of current forest trends in western Iowa by McComb and Loomis (1944) indicated that burr oak was an active and successful prairie invader. *Ulmus* spp. also of considerable

importance in the north were not recorded in the prairies and barrens of Dade County. In this southwest section of the Missouri transition, the main species found in the prairie and barrens were *Quercus stellata* (27 per cent of total tabulation for these areas), *Q. marilandica* (23 per cent), and *Carya* spp. (27 per cent). These species diminished in relative abundance northward along the transition, to 6.1 per cent for *Quercus stellata* and 3.5 per cent for *Carya* spp. in Clark County. *Quercus marilandica* was not recorded for either of the two northern positions. Analysis of composition data indicated that the principal tree associates in the prairie were also the forest dominants in the respective regions.

The distributions of pre-settlement vegetation in Clark, Boone, and Dade Counties are shown in figures 1, 2, and 3. A generally close relationship be-

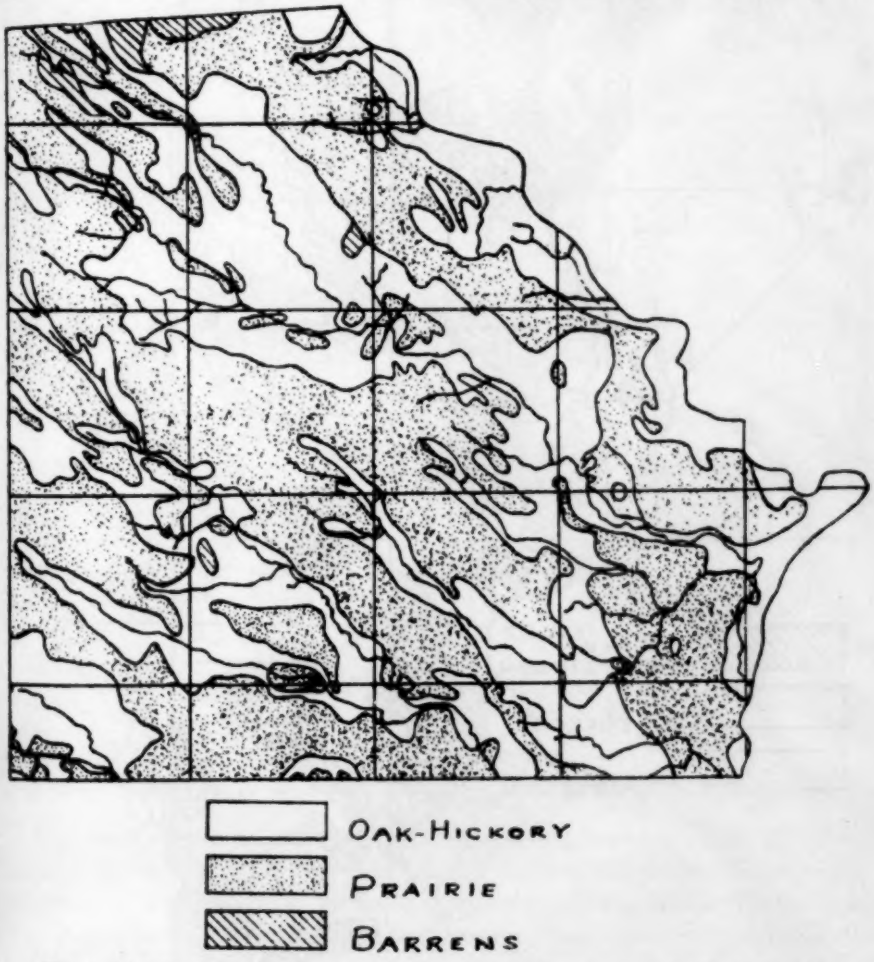

FIG. 1. Distribution of major vegetation types based on surveys in Clark County.

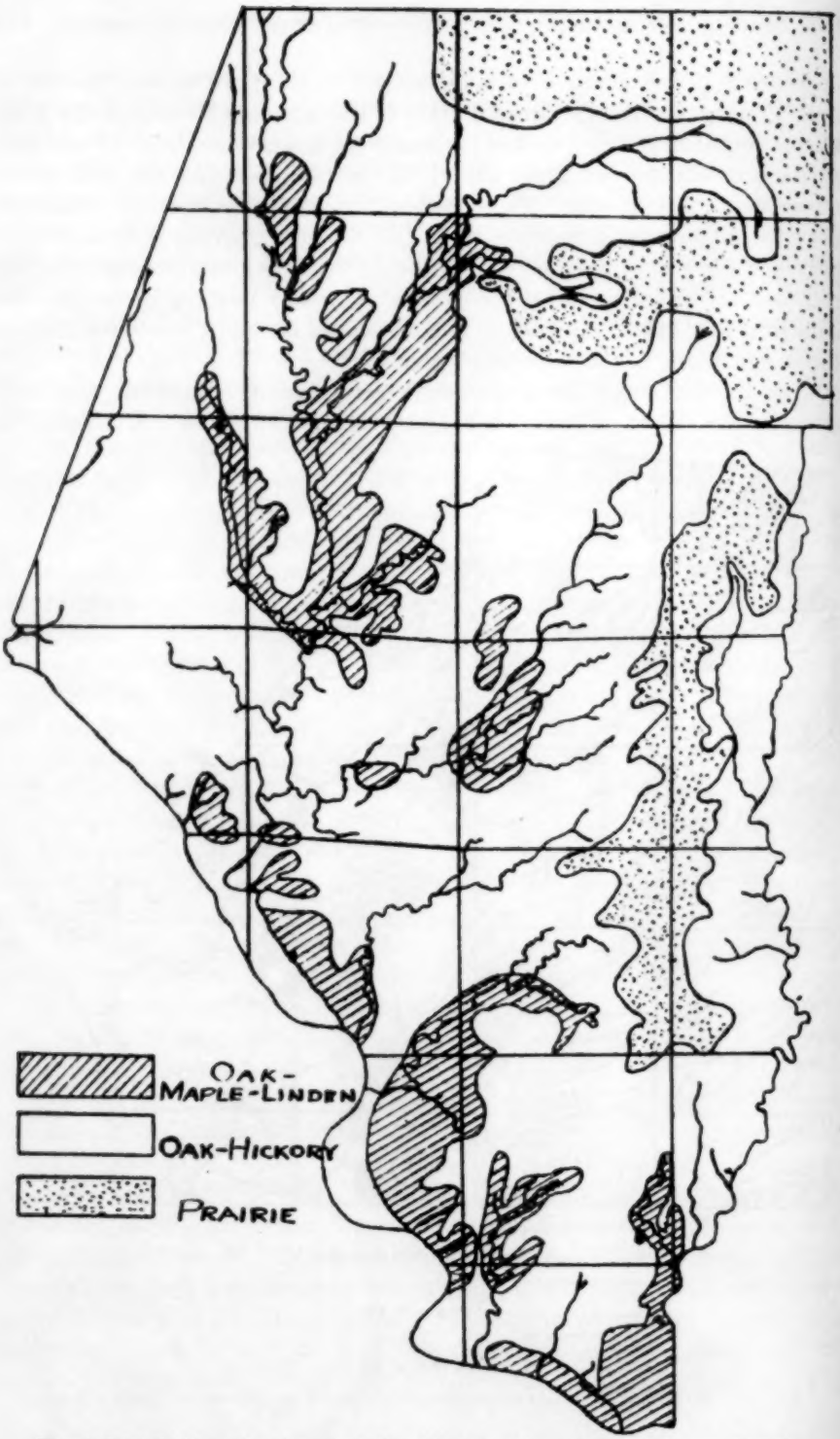

FIG. 2. Distribution of major vegetation types based on surveys in Boone County.

tween forest patterns and the drainage system is apparent. Boone County, the most densely forested of the three study regions, had no areas designated as barrens in the survey. Here, the forest-prairie ecotone was relatively narrow and well-defined. Barrens occurred in the other counties, indicating according to the surveyor widely-spaced trees and the presence of a forb and grass cover.

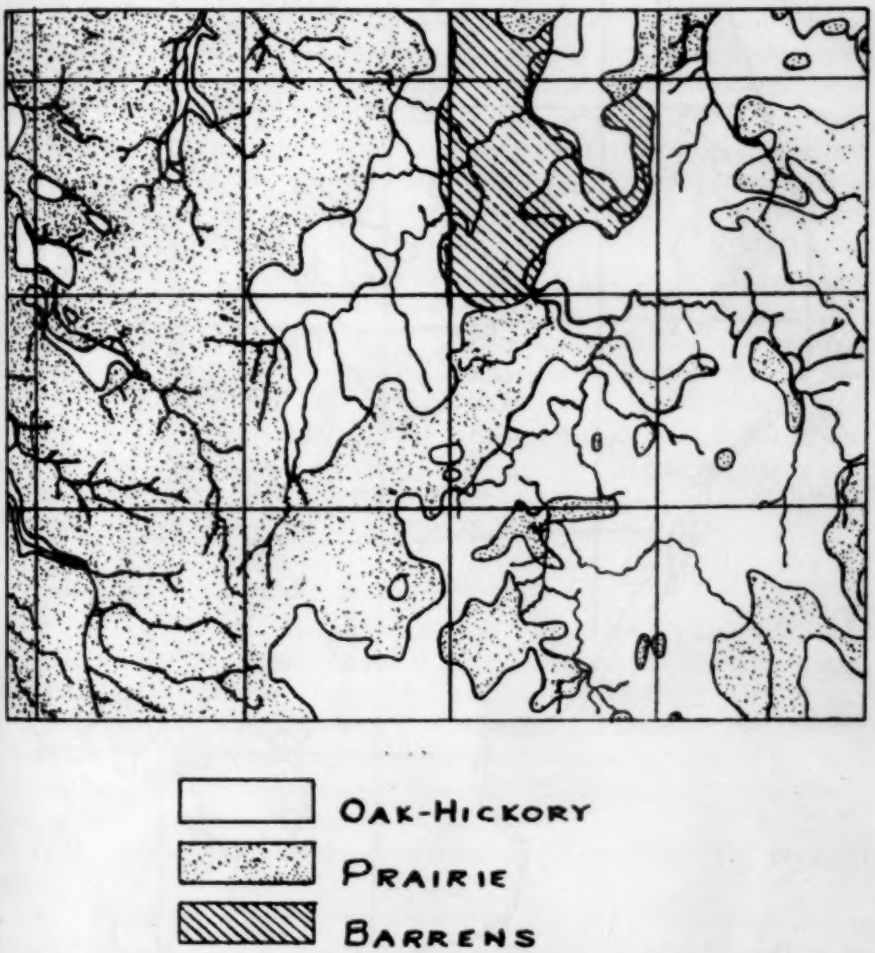

FIG. 3. Distribution of major vegetation types based on surveys in Dade County.

Oak-hickory forest was the most extensive general type in all study regions. As shown previously, the species composition varied, particularly between Dade County in southwestern Missouri and the two northerly counties. Maple-basswood records in Clark County were scattered and relatively

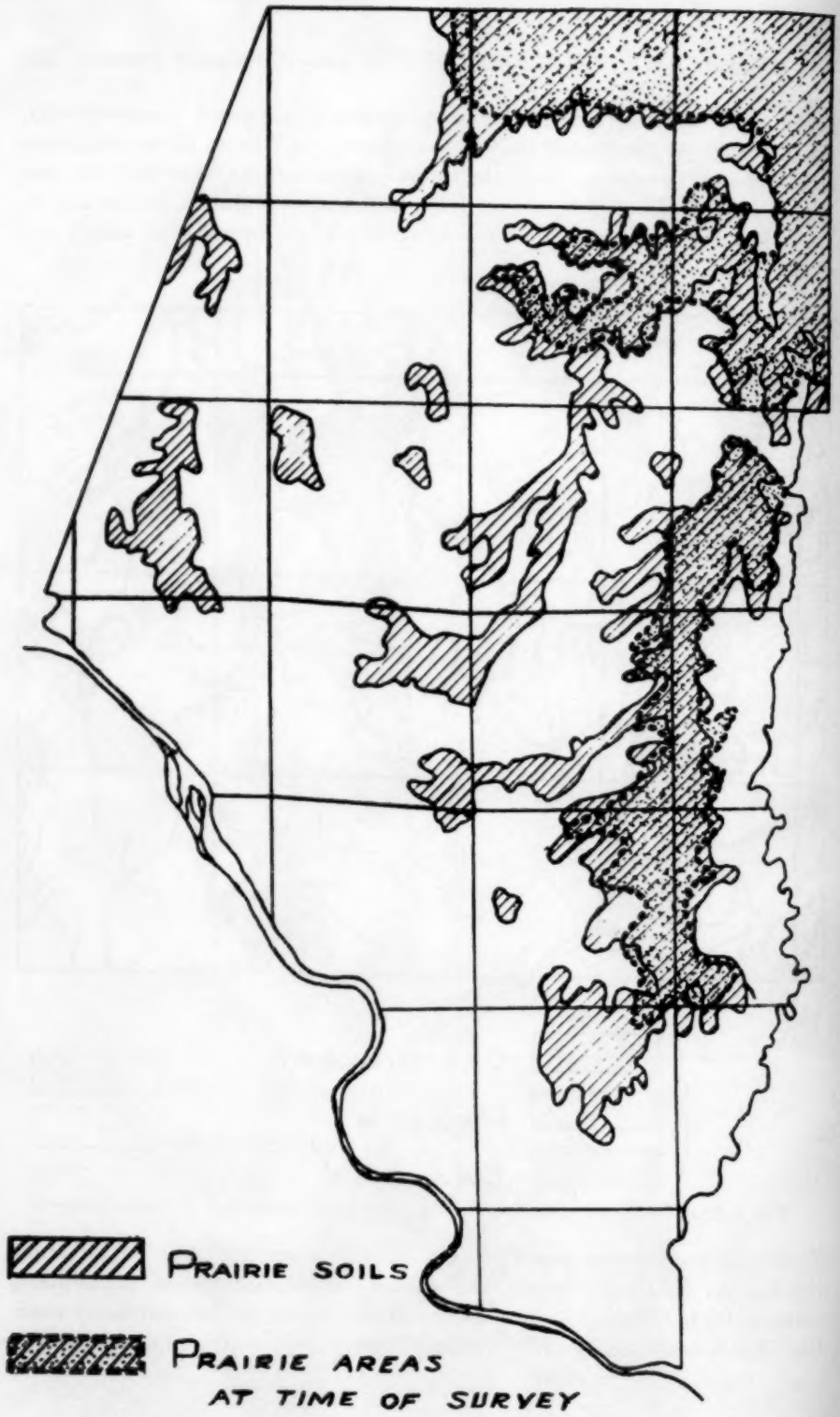

FIG. 4. Forest advance over prairie—formed soils in Boone County.

sparse. In all of Dade County only three maples and one basswood were recorded. Sufficient numbers and concentrations in Boone County made possible, with reference to topographic maps, an estimation of the distribution of this type. The areas in which maple and basswood predominated at the time of survey are characterized by considerable dissection. A rough deep ravine topography is typical. Fragmentary stands of sugar maple, basswood, and red oak which still occur in the river-hill district of the county, have been the subject of composition studies by Kucera and McDermott (1955).

In order to ascertain the condition of the zone of interdigitation between prairie and forest, vegetation boundaries at the time of survey were superimposed on the soils distribution. This was done for Boone County for which such soil information was available (Scrivner and Frieze 1951). The presettlement forest of 140 years ago had encroached on prairie-formed soils (Putman, Mexico, and Seymour silt loans) to a considerable extent, with the ecotone generally well within the limits of the prairie soil (fig. 4). Assuming that the border between prairie-formed soils and those formed under forest represents an earlier competitive zone, the environmental complex has favored the advance of forest communities into habitat formerly occupied by prairie. Observations of a similar nature have been reported elsewhere in Prairie Peninsula studies (Dick-Peddie 1952, Loomis and McComb 1944). Field studies in Boone County indicate present encroachment by forest species, particularly *Ulmus americana*. This current invasion is presumably furthered by soil erosion, gully formation, continuing deterioration of isolated areas of prairie, and the lessened incidence of fire.

SUMMARY

1. The original territorial survey records were utilized in making a study of the distribution and composition of the primeval forests of Clark, Boone, and Dade Counties in the forest-prairie transition of Missouri.

2. A total of 6500 witness trees were recorded and described by the early surveyors. Forty-seven different tree designations were listed with the largest number (38) in Boone County, followed by Clark County (35), and Dade County in southwestern Missouri with 23.

3. *Quercus* spp. constituted approximately 65 per cent of all recorded trees.

4. *Quercus alba* and *Quercus macrocarpa* were the principal oak species of the forests in the central and northern parts of the transition. *Quercus stellata* and *Quercus marilandica* were dominants in the southwest part of the transition in Dade County. This sequence applied also to the principal species recorded in the prairies and barrens of the three counties.

5. Other species of decreasing importance included *Carya* spp., *Ulmus* spp., *Acer saccharum, Celtis occidentalis, Fraxinus* spp. and *Tilia americana*.

Hickory was more important toward the south in the transition whereas toward the north, elm increased in species importance.

6. Oak-hickory was the most common general type in all study positions. Sufficient concentration of sugar maple and basswood with oak afforded mapping of a second type for Boone County. The latter was restricted to dissected, ravine topography associated with the major drainages

7. The most densely wooded areas based on the smallest average distance of witness trees from section corners occurred in Boone County.

8. The largest trees including a 74 inch burr oak were recorded for Boone County.

9. The vegetation—soil relationships of Boone County revealed that at the time of survey, large areas of prairie-formed soils were being invaded by forest.

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CHEMICAL STRAINS OF THE PARMELIA CONSPERSA-STENOPHYLLA GROUP IN SOUTH CENTRAL UNITED STATES[1]

MASON E. HALE, JR.

In a recent publication the author (1955) presented a broad study of the *Parmelia conspersa-stenophylla* lichen group in North America, which was based for the most part on herbarium specimens. The four species in the group were separated by type of adnation and presence of isidia. Members of each species which contained different lichen substances were designated as chemical strains. Since few specimens from south central United States were available in herbaria at the time, the author completed an intensive field study of the group in 1954 and 1955 with the aim of delimiting more accurately the geographic ranges of the chemical strains present there.

A total of 361 collections was made at 45 localities in 40 counties of Missouri, Arkansas, Kansas, Oklahoma, and Texas. The most abundant species, *Parmelia isidiata*, occurred at 82 per cent of the localities, *P. conspersa* at 64 per cent, and *P. stenophylla* at 55 per cent. Six lichen substances, all previously reported for the group, were demonstrated microchemically in the specimens. Their percentage distribution is summarized in Table 1. Norstictic acid was the main component in only the one specimen of *P. isidiata* but usually accompanied stictic acid. Atronorine is strictly an accessory substance.

TABLE 1. *Percentage of species with each of six lichen substances.*

	Number tested	Salacinic acid	Fumarprotocetraric acid	Stictic acid	Norstictic acid	Usnic acid	Atronorine
P. isidiata	186	55%	43%	1.5%	.5%	100%	1%
P. conspersa	119	41	27	32	0	100	0
P. stenophylla	56	82	18	0	0	100	0

Although four chemical strains of *Parmelia isidiata* were recognized, 98 per cent of the material contained either salacinic acid or fumarprotocetraric acid. The latter strain is restricted geographically to sandstone outcrops in

[1] Field work supported by grants from the Sigma Xi-RESA Research Fund and from the American Philosophical Society.

the mixed oak-pine forests of Arkansas, Missouri, and extreme eastern Oklahoma (fig. 1). Within this area salacinic acid was demonstrated in only 3 per cent of the specimens. On the other hand the strain producing salacinic acid inhabited almost exclusively the outcrops in xeric oak woods of the prairie-forest border from southeast Kansas through central Oklahoma into northeast Texas (fig. 1). In this region only 1 per cent of the plants contained fumarprotocetraric acid. A mixed population with both strains was encountered at two localities in east central Oklahoma. The three chemical strains of *P. conspersa* occur in nearly equal proportions at 29 stations in the prairie-

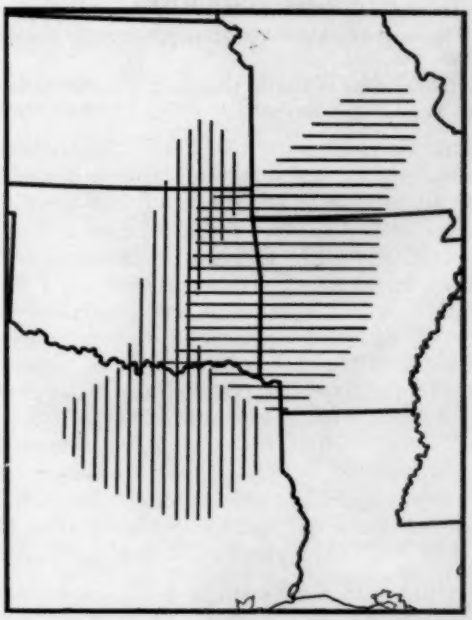

FIG. 1. Distribution of two strains of *Parmelia isidiata* in south central United States. Horizontal lines indicate the range of the fumarprotocetraric acid strain; vertical lines stand for the salacinic acid strain.

forest border and the oak-pine woods. Likewise, the two strains of *P. stenophylla* show no geographic restriction.

The results of this study illustrate interesting patterns of distribution for chemical strains in a small area. The strains of *Parmelia conspersa* and *P. stenophylla* are distributed essentially at random, whereas two strains of *P. isidiata* are confined to specific habitats, the fumarprotocetraric acid strain to more mesophytic woods, the salacinic acid strain to xeric open stands. There are at least two explanations for the existence of such discrete distributional patterns for *P. isidiata*. The two chemical strains may belong to gentically different populations which happen to converge along the

prairie-forest border. It is also possible that production of salacinic and fumarprotocetraric acids is directed by environmental gradients from mesic to xeric woods. In the latter case the strains would likely result from metabolic shunts such as are postulated for the fungus *Blastocladiella* (Cantino 1952). At the present time, however, there is no conclusive proof to support either hypothesis in the lichens.

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DESCRIPTIONS OF TROPICAL RUSTS—VIII[1]

GEORGE B. CUMMINS

In this paper 23 new rust fungi are described. Of the 23 species 15 are from Africa, six are from the Americas and two are from the Pacific area. There are 19 grass rusts. Following the designation of the type the deposition of type material is indicated as follows: A. H. = Arthur Herbarium; C. M. I. = Commonwealth Mycological Institute; Kew = Royal Botanic Gardens; Oslo = Botanical Museum, Oslo; U. S. D. A. = National Fungus Collections, United States Department of Agriculture.

Angiopsora africana sp. nov. Urediis amphigenis, sparsis, ellipticis, 0.2–0.4 mm. longis, flavo-brunneis, pulverulentis, epidermide rupta conspicue, paraphysibus peripheralibus incurvatis haud conspicuis, hyalinis vel pallide flavidis, 10–15 × 30–55 μ, membrana in parte interiore 1 μ cr., exteriore 2–3 μ cr.; urediosporis ellipsoideis vel ovoideis (14–) 16–20 (–23) × (23–) 26–33 (–36) μ; membranis 1.5 μ cr., echinulatis, hyalinis vel pallide flavo-brunneis, poris germ. obscuris verisimiliter 4, equatorialibus. Teliis amphigenis, subepidermalibus, indehiscentibus, sparsis vel seriatim dispositis et frequenter confluentibus, oblongis vel linearibus, 0.2–1.0 mm. longis, brunneis, ex sporis 2 vel 3 catenulatim compositis; teliosporis plerumque oblongis, 10–16 × (16–) 20–26 (–29) μ, membrana 2 μ cr. ad apicem ad 3 μ cr., aureo-/vel pallide castaneo-brunnea, levi.

On *Brachiaria brizantha* (Hochst.) Stapf, Nairobi, Kenya, Sept. 9, 1929, *Hitchcock 24726*, Kipago, Uganda, June 1914, *Dummer 895*, Fort Portal, Uganda, Feb. 1929, *Hansford 1005;* on B. *decumbens* Stapf, Kabale, Kigezi, Uganda, Aug. 1937, *Hansford 2178* Type: (A.H., C.M.I.).

A. africana has larger urediospores than any other species known on the Paniceae except *A. phakopsoroides* (Arth. et Mains) Mains but it has smaller (8–14 × 11–18 μ) teliospores. Other species which have dorsally thick-walled paraphyses are *A. clemensiae* Arth. et Cumm., *A. compressa* Mains, *A. hansfordii* Cumm., and *Angiopsora digitariae* Cumm.

Angiopsora aurea sp. nov. Urediis amphigenis vel plerumque epiphyllis, laxe aggregatis, flavidis, pulverulentis, ellipticis, 0.1–0.3 mm. longis, paraphysibus nullis; urediosporis ovoideis, (14–) 16–19 × 22–26 (–29) μ, membrana hyalina, echinulata, 1μ cr., poris germ. obscuris, verisimiliter sparsis. Teliis hypophyllis, subepidermalibus, indehiscentibus, aureo-brunneis, ellipticis vel oblongis, 0.2–1.0 mm. longis, ex sporis 3–6 catenulatim compositis;

[1] Cooperative investigations between the Purdue University Agricultural Experiment Station and the Plant Disease Epidemics and Identification Section, Agricultural Research Service, United States Department of Agriculture. Journal Paper Number 927, of the Purdue University Agricultural Experiment Station. Contribution of the Department of Botany and Plant Pathology.

teliosporis oblongis, 8–13 × 14–20 μ, membrana uniformiter 1 μ cr., hyalina vel pallide flava, levi.

On *Panicum olivaceum* Hitchc. et Chase, Uyuca, Honduras, Jan. 13, 1951, *A. S. Müller 419* Type: (A.H.), on *P. sphaerocarpon* Ell., slopes of Cerro de Uyuca, Dept. Morazan, Honduras, Feb. 22, 1947 *Standley* and *Molina 4177*, Dec. 8, 1946, *Standley, Allen, Shank* and *Padilla 946*.

This species differs from all others in having teliospores with uniformly thin colorless walls. The telia are brownish when dry but probably are golden or orange when fresh. Telia have not been seen on *Panicum sphaerocarpon*.

Angiopsora digitariae sp. nov. (*Melampsora syntherismae* Sawada in Taiwan Agr. Res. Inst. **87**: 44. 1944 *nom. nud.*). Urediis plerumque hypophyllis, minutis, ca. 0.1 mm. diam., flavidis, pulverulentis, paraphysibus peripheralibus, incurvatis, hyalinis vel pallide flavidis, 8–11 × 25–40 μ, membrana in parte interiore 1–1.5 μ cr. in parte exteriore 3–5 μ cr.; urediosporis plus minusve ovatis, 15–20 × (18–) 21–26 (–28) μ, membrana 1–1.5 μ cr., hyalina vel pallide flavida, echinulata, poris germ. obscuris verisimiliter sparsis. Teliis hypophyllis, sparsis, subepidermalibus, indehiscentibus, oblongis, 0.2–0.8 mm. longis, atro-brunneis; teliosporis unistratosis, oblongis vel oblongo-ellipsoideis, (7–) 9–11 (–13) × (16–) 20–25 (–30) μ; membrana aureo-brunnea, uniformiter 1–2 μ cr., levi.

On *Digitaria chinensis* Hornem. (*D. formosanum* Honda), Taipeh, Formosa, Nov. 22, 1913, *K. Sawada* Type: (A.H., U.S.D.A.)

The relationships of this species are not obvious. Since no telia were found to be more than one spore in depth it could be placed in *Melampsora*, as done by Sawada. However, the paraphyses are not melampsoroid but typical of those found in *Angiopsora* and *Phakopsora*.

Sawada (*l.c.*) also cited *Ischaemum ciliare* Retz as a host but the rust is doubtless *Phakopsora incompleta* (Syd.) Cumm. Since Sawada's description of *M. syntherismae* was in Japanese the binomial was not validly published and the epithet cannot be transferred.

Hapalophragmium deightonii sp. nov. (fig. 1). Spermogoniis et aeciis ignotis. Urediis et teliis subepidermalibus, cinnamoneo-brunneis, plus minusve pulverulentis, denseque sparsis, minutis, 0.1–0.3 mm. diam., paraphysibus peripheralibus valde incurvatis, aureobrunneis, 6–10 × 20–35 μ membrana in parte interiore 0.5–1.0 μ cr., urediosporis plerumque obovatis, 18–22 × 23–28 (–30) μ, membrana 1–1.5 μ cr., cinnamomeo-brunnea, poris germ. 2, equatorialibus; teliosporis plus minusve triangulariter 3-cellularibus, (23–) 26–30 (–33) × (32–) 38–45 (50) μ, quaque cellula plus minusve ellipsoidea et poro germ. singulo juxta apicem praedita, membrana flavido- vel aureo-brunnea, 0.5–1 μ cr. ad apicem papilliformiter incrassato 3–5 μ, levibus; pedicello hyalino, brevi, juxta apicem uniseptato; statim germ.

On *Millettia barterii* (Benth.) Dunn, Musaia, Sierra Leone, Dec. 17, 1946, *F. C. Deighton 2554* Type: (A.H., C.M.I.).

This species differs from *H. millettiae* Syd. and *H. millettiae-rhodanthae* Viennot-Bourgin in having urediospores with uniformly thin walls. Each

cell of the teliospore is free in its apical portion and the apex is abruptly narrowed into a thick-walled or usually solid mammiform papilla. The germ pore in each cell is situated at the base of the papilla. The pedicel, just below its union with the teliospores, is 1-septate as in *Dicheirinia*.

Phakopsora loudetiae sp. nov. Urediis amphigenis, sparsis vel laxe aggregatis, pulverulentis, cinnamomeo-brunneis, ellipticis, 0.3–1.0 mm. longis, paraphysibus peripheralibus flavo-brunneis, 8–11 × 35–55 μ, membrana 1–2 μ cr., in parte exteriore 3–5 μ cr., ad apicem usque 12 μ cr.; urediosporis obovoideis vel ellipsoideis, (15–) 18–21 (–23) × (24–) 26–32 (–34) μ, membrana 1–1.5 μ cr., echinulata, flavo-brunneis, poris germ. obscuris sed 7–9 sparsis. Teliis plerumque hypophyllis, subepidermalibus, indehiscentibus, atro-brunneis, sparsis vel laxe aggregatis, ellipticis vel oblongis 0.2–0.5 mm. longis, ex sporis 2–4 irregulariter superpositis compositis; teliosporis ellipsoideis vel plus minusve oblongis, 14–18 × 16–28 μ, membrana 2 μ cr. vel ad apicem 2–3 μ cr., aureo-brunnea, levi.

On *Loudetia arundinacea* (Hochst.) Steud., Omia Anyema, Uganda, June 30, *Liebmbing 23* Type: (A.H., U.S.D.A.); on *L. kagerensis* (K. Schum.) C. E. Hubb., Nairobi, Kenya, June 1950, *R. M. Nattrass 1398*, Kisumu, Kenya, Sept. 15, 1929, *Hitchcock 24855*, Entebbe, Uganda, Sept. 16, 1929, *Hitchcock 24873*.

This is the first species of *Phakopsora* recorded as parasitizing grasses of the tribe Aveneae. The uredia are not yellowish or golden as in other graminicolous species but are brown.

Phakopsora oplismeni sp. nov. (*Uredo oplismeni* Arth. et Cumm. in Phil. Jour. Sci. **59**: 442. 1936. *Phakopsora oplismeni* Cumm. in Mycologia **33**: 143. 1941 *nom. nud.*). Teliis hypophyllis, sparsis, erumpentibus, ovalibus vel elongatis, 0.3–1.0 mm. longis, aureo-brunneis, ex sporis 3–8 irregulariter superpositis compositis; teliosporis ellipsoideis, oblongis vel cuboideis, 9–16 × 14–23 μ, membrana hyalina vel pallide flavida, uniformiter 0.5–1 μ cr., levi; statim germ.

On *Oplismenus compositus* (L.) Beauv., Kajabit Mission, New Guinea, Aug. 12, 1939, *M. S. Clemens 10568* Type: (A.H.), on *O. undulatifolius* (Ard.) P. Beauv., Mt. Santo Tomás, Benguet Subprov., Luzon, Feb. 19, 1925, *M. S. Clemens 5786* (type of *Uredo oplismeni* Arth. et Cumm.).

Cummins' original description of the telial stage was in English, hence the name was not validated by that publication.

P. *oplismeni* is unique in that the telia are not long-covered by the epidermis of the host.

Phakopsora setariae sp. nov. Urediis amphigenis, sparsis vel laxe aggregatis, ovatis vel ellipticis, 0.1–0.4 mm. longis, flavidis vel flavo-brunneis, pulverulentis; paraphysibus peripheralibus pallide flavidis, incurvatis, 8–13 × 25–50 μ, membrana in parte interiore 1.5–3 μ cr. in parte exteriore 3–6 μ cr.; urediosporis ellipsoideis vel obvoideis, 15–18 × 22–27 (–29) μ, membrana 1–1.5 μ cr., hyalina vel pallide flavida, echinulata, poris germ obscuris, verisimiliter sparsis. Teliis amphigenis, sparsis vel aggregatis, rufo- vel atro-brunneis, subepidermalibus, indehiscentibus, ovalibus vel

oblongis, 0.1–0.8 mm. longis, ex sporis 2–4 irregulariter superpositis compositis; teliosporis oblongis vel ellipsoideis, 11–15 × (16–) 20–26 (–30) μ, membrana aureo-brunnea, 1–1.5 μ cr. vel ad apicem 1–2.5 μ cr., levi.

On *Setaria aequalis* Stapf, Kampala, Uganda, Feb. 1930, *Hansford 1059;* on *S. lancea* Stapf, Juba, Sudan, Oct. 1952, *J. Tarr 1908* Type: (A.H., C.M.I); on *S. sphacelata* (Schum.) Stapf et C. E. Hubb., Zomba Plateau, Nyasaland, Feb. 24, 1949, *Wiehe 43a.*

This species differs from *P. apoda* (Hariot et Pat.) Mains in having shorter and narrower urediospores and a thinner apical wall in the outer teliospores. *P. apoda* parasitizes species of *Pennisetum.* Wakefield and Hansford (Proc. Linnaean Soc. London **161**: 163. 1949), on the basis of uredia only, reported Hansford No. 1059 as *P. apoda.*

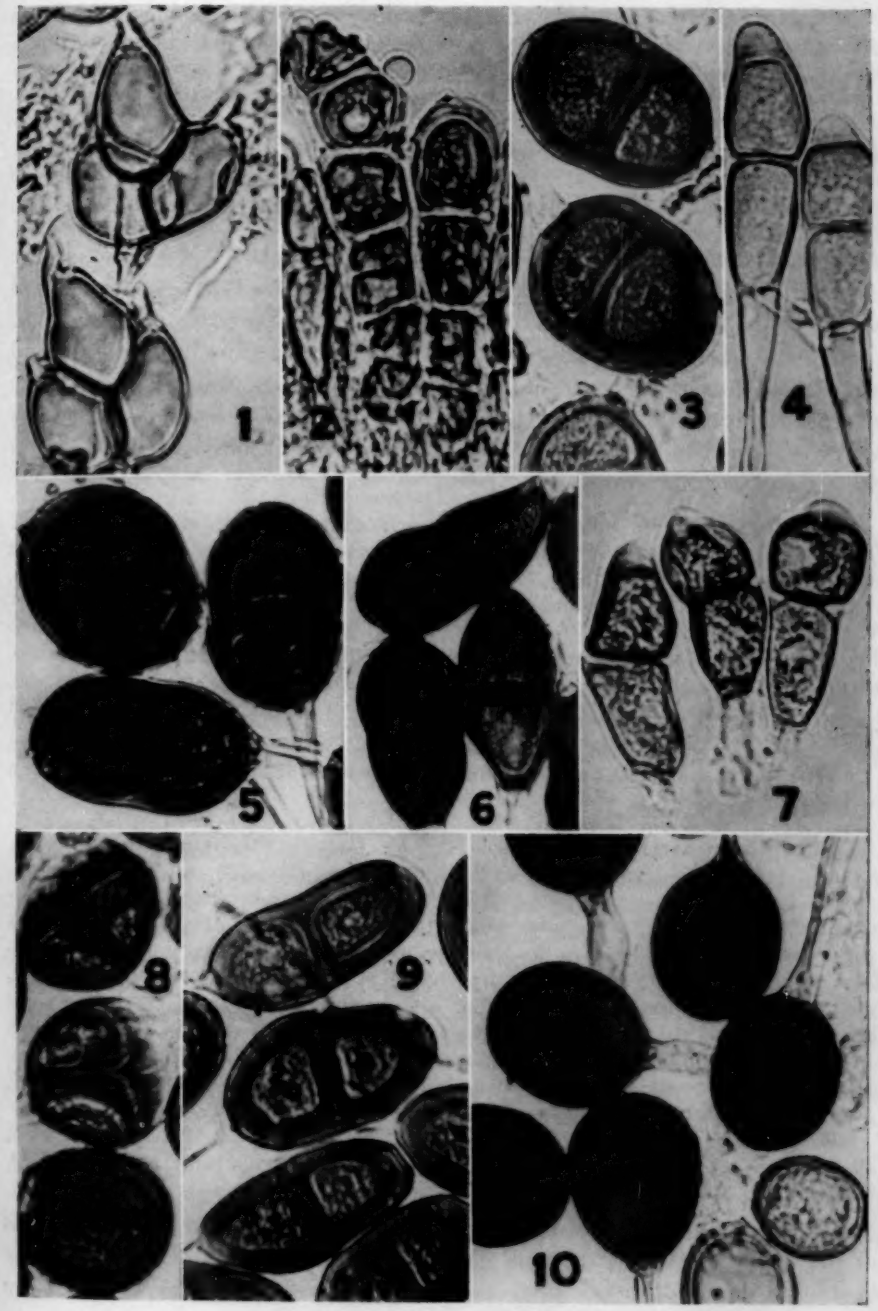
Phragmidiella (?) **ugandana** sp. nov. (fig. 2). Urediis hypophyllis, subepidermalibus sparsis, 0.1–0.3 mm. diam., cinnamomeo-brunneis, pulverulentis, paraphysibus nullis; urediosporis obovoideis vel plus minusve globoideis, 16–20 × 19–23 μ, membrana cinnamomeo-brunnea, 1.5–2 μ cr., echinulata, poris germ. 3, equatorialibus. Teliis subepidermalibus dein erumpentibus, compactis, brunneis vel atro-brunneis, usque ad 0.35 mm. diam., usque ad 145 μ crassa, ex cellulis 3–8 catenulatim compositis; teliosporis oblongis vel cuboideis 13–18 × 14–24 (–30) μ, in catenas elongatas connexis, lateraliter non vel vix connexis, levibus, membrana 2–3 μ cr., flavida vel aureo-brunnea.

On *Trichilia* sp., Serere, Teso, Uganda, Feb. 1933, *C. G. Hansford 1625* Type: (A.H., Kew).

This is a species of uncertain relationships. When telia develop separately they are crustose and the chains of spores are closely compacted but it is doubtful if the chains are actually laterally adherent. When such telia have ruptured the epidermis and become erumpent the apical portions of the chains are obviously free. When development occurs within a uredium the chains are laterally free and frequently isolated among the old urediospore pedicels. They then are definitely spore-like (fig. 2) and resemble somewhat the teliospores of *Xenodochus* or *Frommea.* An occasional unit of a spore chain may be two cells wide because of a vertical septum.

Previously described species of *Phragmidiella* parasitize bignoniaceous hosts.

FIGS. 1–10. FIG. 1. Teliospores of *Hapalophragmium deightonii.* (From type). FIG. 2. Teliospores of *Phragmidiella ugandana* developing in an uredial sorus. When produced in separate telial sori the spore chains are similar but more compacted laterally. (From type.) FIG. 3. Teliospores of *Puccinia bewsiae.* (From type.) FIG. 4. Teliospores of *Puccinia cissi.* (From type.) FIG. 5. Teliospores of *Puccinia hyparrheniae.* (From type.) FIG. 6. Teliospores of *Puccinia loudetiae-superbae.* (From type.) FIG. 7. Teliospores of *Puccinia millegranae* (From type.) FIG. 8. Teliospores and one urediospore of *Puccinia nyasaensis.* (From type.) FIG. 9. Teliospores of *Puccinia nyasalandica.* (From type.) FIG. 10. Teliospores and urediospores of *Puccinia perotidis.* (From type.) × 800.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Puccinia bewsiae sp. nov. (fig. 3). Urediis et urediosporis ignotis. Teliis erumpentibus culmicolis et inflorescenticolis, elongatis, 0.5–4.0 mm. longis vel confluentibus, pulvinatis, compactis, castaneo-brunneis; teliosporis ellipsoideis, utrinque rotundatis vel deorsum lenissime attenuatis, medio non vel vix constrictis, (22–) 24–29 (–32) × (32–) 34–39 (–41) μ, membrana 2.5–3.5 (–4) μ ad apicem 5–7 (–9) μ cr., aureo-vel lucide castaneo-brunnea, levi; pedicello hyalino, tenue tunicato, semipersistenti, usque ad 90 μ longo vel verissimiliter longiore.

On *Bewsia biflora* (Hack.) Goosens, Dezda, Nyasaland, Sept. 1950, *G. Jackson* (comm. P.O. Wiehe as No. 888, Type:) (A.H., C.M.I.).

In the absence of uredia and urediospores it is more than usually difficult to determine the relationships of this species. It is generally similar to *Puccinia pogonarthriae* Hopkins but the latter has considerably shorter and particularly narrower teliospores (19–25 × 28–36 μ). Moreover, the germ pore of the lower teliospore cell is at the septum in *P. bewsiae* but in the lower one-third of the cell in *P. pogonarthriae*. The hosts of both species are members of the Festuceae.

Puccinia cissi sp. nov. (fig. 4). Spermogoniis, aeciis et urediis nullis. Teliis hypophyllis, erumpentibus, in greges usque ad 5 mm. diam. denseque aggregatis, cinereo-brunneis, compactis; teliosporis plerumque oblongis, utrinque rotundatis vel lenissime contractis, medio vix constrictis, (12–) 15–17 (–19) × (34–) 38–50 (–53) μ; membrana flavida vel pallide aureo-brunnea, 1 μ cr. ad apicem 5–9 μ cr.; pedicello tenuiter tunicato, hyalino, usque ad 10 μ lato, 60 μ longo, persistenti; statim germ.

On *Cissus sp.*, Uplands 7900 ft., Kenya, Oct. 1950, *R. M. Nattrass 1548* Type: (A.H., C.M.I.).

This microcyclic fungus is the first species of *Puccinia* reported on Vitaceae.

Puccinia hyparrheniae sp. nov. (fig. 5). Urediis plerumque hypophyllis, sparsis vel seriatim dispositis et confluentibus, flavidis, epidermide semitectis, pulverulentis, elongatis, 0.5–2.0 mm. longis, paraphysibus nullis; urediosporis ovoideis vel obovoideis, (22–) 24–27 (–29) × (25–) 27–33 (–35) μ, membrana 1–1.5 μ cr. ad apicem abrupte incrassata 10–19 μ, hyalina, echinulata, poris germ. obscuris, 3 vel 4 juxta partem incrassatam dispositis. Teliis urediis conformibus ser atro-brunneis et pulvinatis; teliosporis late ellipsoideis, utrinque rotundatis, medio haud constrictis, (23–) 25–28 (–30) × (36–) 38–44 (–46) μ, membrana 3–4 μ cr. ad apicem usque ad 5.5 μ, aureo- vel lucide castaneo-brunnea, levi; pedicello hyalino, tenue tunicati, persistenti, usque ad 90 μ longo.

On *Hyparrhenia rufa* (Nees) Stapf, Zomba plateau, Nyasaland, Feb. 20, 1949, *Wiehe 20*, on *H. variabilis* Stapf, Zomba, Nyasaland, May 24, 1949, *P. O. Wiehe 222* Type: (A.H., C.M.I.).

The urediospores of this rust are striking because of the great thickness of the apical region of the wall. Approximately half of the length of the spore is composed of the thickened region, immediately below which are situated the pores. This rust was mentioned (Uredineana 4: 46. 1953) in

connection with but probably as being distinct from *P. eucomi* Doidge. The apical wall of the urediospores is much thinner (5–8 μ) in *P. eucomi* whose teliospores are of the same general size and shape but have the apical wall 5–9 μ in thickness.

Puccinia hyparrheniicola Joerst. et Cumm. sp. nov. (fig. 14). Urediis hypophyllis, castaneo-brunneis, pulverulentis, 0.4–2.0 mm. longis vel seriatem confluentibus, paraphysibus copiosis geniculatis vel incurvatis, aureo-brunneis, 8–18 μ latis usque ad 70 μ longis, crasse tunicatis 3–6 μ vel ad apicem usque 10 μ; urediosporis late ovatis vel plus minusve globoideis (21–) 24–27 (–29) × (26–) 28–31 (–34) μ, membrana (1.5–) 2–3 μ cr., obscure cinnamomeo- vel castaneo-brunnea, echinulata, poris germ. 6–8, sparsis. Teliosporis in urediis oblongis vel oblongo-ellipsoideis, medio haud constrictis, 16–19 (–22) × (28–) 33–40 (–45) μ, membrana 1 (–1.5) μ cr. ad apicem (2.5–) 3–3.5 (–4) μ cr., lucide aureo-brunnea vel ad apicem pallidiore, levi; pedicello hyalino, tenue tunicati, usque ad 15 μ longo.

On *Hyparrhenia hirta* (L.) Stapf, Canary Islands: near Santa Cruz, Tenerife, Mar. 21, 1954 *I. Jørstad 822* Type: (A.H., Oslo) Taoro, Tenerife, Jan. 29, 1954, *Jørstad 66,* Bco. Santa Lucia, La Palma, Mar. 6, 1954, *Jørstad 547.*

Both the type and No. 547 have teliospores. The species has paler teliospores with the side wall much thinner than described for *Puccinia andropogonis-hirti* Beltrán. Moreover, the pore is described as situated midway to the pedicel in *P. andropogonis-hirti* while it is next to the septum in *P. hyparrheniicola.* The apical pore of the latter is covered by a low umbonate thickening while each pore in the former is under a small papilla. Without teliospores it is doubtful whether these two species and *P. erythraeensis* Paz. can be distinguished.

Puccinia loudetiae-superbae sp. nov. (fig. 6). Urediis amphigenis, sparsis vel plus minus seriatem dispositis, pulverulentis, cinnamomeo-brunneis, ellipticis vel linearibus, 0.5–1.0 mm. longis, paraphysibus hyalinis vel flavidis, capitatis, 12–22 μ latis usque ad 55 μ longis, membrana 1–2 μ crassa ad apicem 6–9 μ cr.; urediosporis ellipsoideis vel obovoideis, 18–21 × (21–) 23–28 μ, membrana 1.5 μ crassa, obscure cinnamomeo-vel castaneo-brunnea, echinulata, poris germ. 3 aequatorialibus. Teliis urediis conformibus sed atro-brunneis, pulvinatis; teliosporis clavatis, ellipsoideis vel oblongo-ellipsoideis, ad apicem plerumque rotundatis deorsum plerumque contractis, medio leniter constrictis, (16–) 18–21 (–23) × (29–) 33–42 (–46) μ, membrana intense castaneo-brunnea, 1.5–2.5 (–3) μ ad apicem 4–6 μ cr., levi, pedicello hyalino flavido, tenue tunicato, persistenti, usque ad 50 μ longo.

On *Loudetia superba* De Not., Morshet Kasupe, Nyasaland, June 16, 1949, *P. O. Wiehe 278* Type: (A.H., C.M.I.), region Lunda, Cacolo, Angola, Apr. 1936, *Grossweiler 11753.*

Most of the rusts of Aveneae have long-covered telia and urediospores with scattered pores. Two, *P. loudetiae* Wakef. et Hansf. and perhaps *P. tristachyae* Doidge have early erumpent telia, paraphysate uredia, and urediospores with equatorial pores. *P. loudetiae-superbae* differs from both

because of its deeply pigmented teliospores whose apical wall is considerably thickened. Its urediospores are also considerably shorter on the average.

Puccinia millegranae sp. nov. (fig. 7). Urediis hypophyllis, sparsis, flavidis, pulverulentis, ellipticis, 0.4–0.8 mm. longis; paraphysibus nullis; urediosporis ovatis vel ellipsoideis, (17–) 21–24 × (24–) 26–30 (–34) μ, membrana 1 μ cr., hyalina vel flavida, echinulata, poris germ. obscuris, sparsis, 3 equatorialibus. Teliis urediis conformibus sed flavo-brunneis et pulvinatis; teliosporis variabilibus, plerumque oblongo-ellipsoideis vel ellipsoideis, utrinque plus minus contractis, ad apicem plus minusve conico-attenuatis, medio haud vel leniter constrictis, 15–19 (–21) × (30–) 35–43 (–46) μ; membrana 1 μ cr. ad apicem 4–7 μ cr., flavida vel lucide aurea, levi; pedicello hyalino, tenue tunicato, usque ad 45 μ longo, fragili, semi-persistenti; statim germ.

On *Panicum millegrana* Poir., Reserva Florestal, Itatiaya, Rio de Janerio, Brazil, May 9, 1922, *E. W. D.* & *Mary M. Holway 1834* Type: (A.H.) (Reliq. Holw. No. 144 as *Puccinia flaccida* Berk. et Br.).

This species is perhaps nearest to *P. puttemansii* P. Henn. but has more elongate and much paler teliospores. The side wall is thinner and the apex conically papillate rather than broadly rounded and umbonately thickened.

Holway's notes indicate that he considered the rust to be quite distinctive in the field: "—a most unusual rust on this."

Puccinia nyasaensis sp. nov. (fig. 8). Urediis non visis, urediosporis late ovatis vel plus minus globosis, (22–) 24–26 (–28) × (26–) 28–32 μ, membrana intense rufo-castanea, (2–) 2.5–3 μ cr., sparse minuteque echinulata, vel apparenter levibus, poris germ. obscuris, 3 equatorialibus. Teliis amphigenis, sparsis, pulvinatis, atro-brunneis, ellipticis, 0.3–1.0 mm. longis; teliosporis diorchidioideis, septo verticali raro horizontali instructis, late ellipsoideis vel plus minusve late obovoideis, 24–33 μ lata, 24–28 (–32) μ alta, membrana 1.5–2 μ ad apicem 5–7 μ cr., castaneo-brunnea, levi; pedicello hyalino, fragili, usque ad 45 μ longo plerumque deciduo.

On *Panicum pectinatum* Rendle, Mlanje, Chambe plateau, Nyasaland, Nov. 15, 1949, *P. O. Wiehe 467* Type: (A.H., C.M.I.).

P. nyasaensis is distinct from other diorchidioid species on Paniceae because of the intensely pigmented almost opaque urediospores which are smooth or nearly so. The rust is on leaves of the previous season and since the urediospores have not germinated they may be amphisporic. If this is true there are no regular urediospores in the collection. Other diorchidioid species which have equatorial pores and parasitize species of *Panicum* or closely related hosts include: *Diorchidium* (= *Puccinia*) *brachiariae* Wakef. et Hansf, *Triphragmium* (= *Puccinia*) *graminicola* Beeli, *Puccinia levigata* (Syd. et Butl.) Hirat. f., *P. levis* (Sacc. et Bizz.) Magn., *P. negrensis* P. Henn., *P. orientalis* (Syd. et Butl.) Arth. et Cumm., *P. pangasinensis* Syd. ex Cumm. (non-valid name but probably = *P. taiwaniana*), and *P. taiwaniana* Hirat. f. et Hash.

Puccinia nyasalandica sp. nov. (fig. 9). Urediis non visis, urediosporis in teliis paucis, ovatis vel fere globosis, 14–18 × 19–21 μ, membrana 1 μ cr.,

hyalina, minuteque echinulata, poris germ. obscuris. Teliis epiphyllis, sparsis vel dense aggregatis, 0.5–2 mm. longis vel valde confluentibus, pulvinatis, obscure brunneis; teliosporis ellipsoideis vel oblongo-ellipsoideis, utrinque rotundatis, medio haud constrictis, 17–20 (–22) × (25–) 30–38 μ, membrana 3–4 μ cr. ad apicem 4–5 (–6) μ cr., aureo-brunnea, levi, poris germ. in cellulis superioribus apicalibus, inferioribus prope hilum dispositis; pedicello hyalino, tenue tunicato, persistenti vel fragili, usque ad 85 μ vel verisimiliter longiore.

On *Brachiaria decumbens* Stapf, Muso, Kirk Range, Nyasaland, June 13, 1950, *P. O. Wiehe 752* Type: (A.H., C.M.I.).

This is one of the relatively few grass rusts in which the pore of the lower teliospore cell is strongly depressed. The pedicel is narrow, tapered basally and rather fragile, hence may be very long when intact. Only a very few urediospores were seen but it is probable that the pores are several and scattered.

Puccinia pappophori sp. nov. (fig. 11). Uredii amphigenis vel plerumque epiphyllis, sparsis, pulverulentis, cinnamomeo-brunneis, ellipticis vel linearibus, 0.4–1.0 mm. longis, paraphysibus nullis; urediosporis ovatis, ellipsoideis vel late ellipsoideis, (22–) 24–29 × 31–38 μ, membrana cinnamomeo-brunnea, echinulata, 1.5 μ cr., poris germ. 4 aequatorialibus. Teliis urediis conformibus sed atro-brunneis, pulvinatis; teliosporis plerumque ellipsoideis vel oblongo-ellipsoideis, utrinque rotundatis, medio non vel vix constrictis, (16–) 18–23 (–25) × (26–) 29–36 (–39) μ, membrana 2–3 μ cr. ad apicem 3–6 μ, castaneo-brunnea, levi; pedicello persistenti, flavido, plus minusve crasse tunicato, usque ad 85 μ longo, raro longiore.

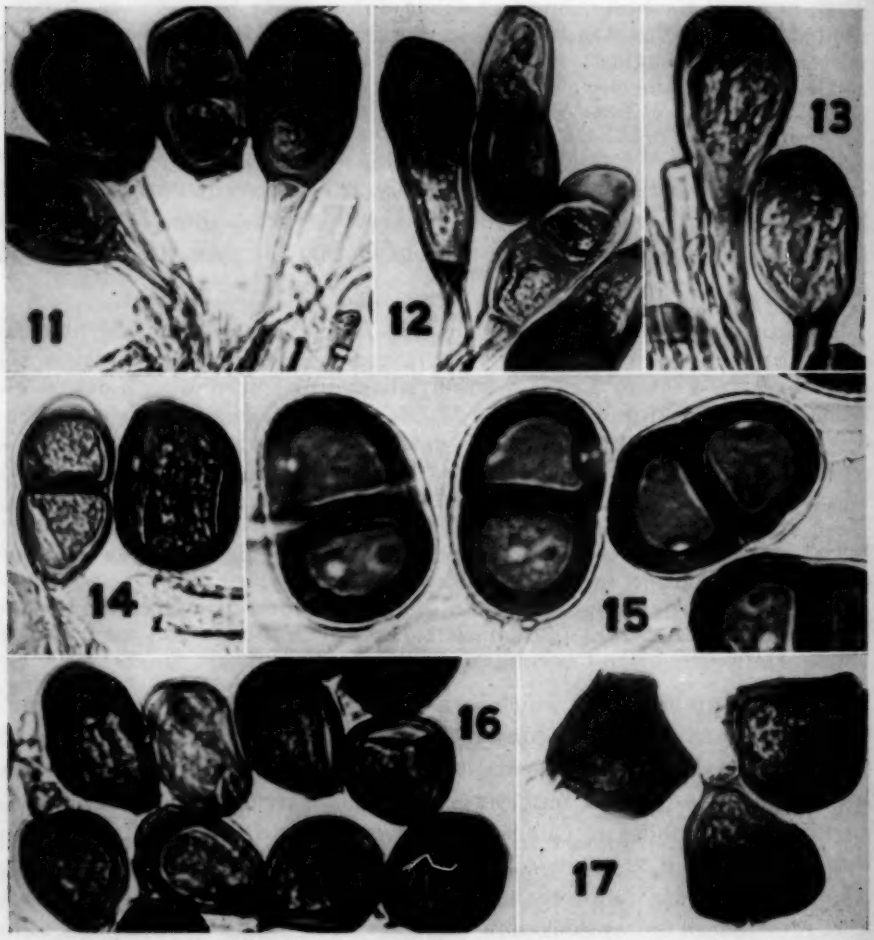
On *Pappophorum mucronulatum* Nees (*P. vaginatum* Buckl.), Cochabamba, Bolivia, Mar. 4, 1920, *E. W. D. & Mary M. Holway 367* Type: (A.H.) (Reliq. Holw. No. 59 as *Puccinia gymnotrichis* P. Henn.).

In the group of species which lack uredial paraphyses, but have echinulate urediospores usually or constantly exceeding 30 μ in length, equatorial pores, and teliospores with pedicels exceeding 25 μ but usually less than 100 μ are *P. arthurii* Syd. on *Pennisetum*, *P. gymotrichis* P. Henn. on *Pennisetum*, *P. kawandensis* Cumm. on *Chrysopogon*, *P. opipara* Cumm. on *Oplismenus*, and *P. cryptandri* Ell. et Barth. (*P. simulans*) on *Sporobolus*. All of these species, however, have larger mostly longer teliospores with a more pronounced apical thickening and most have smaller urediospores than does *P. pappophori*.

Puccinia perotidis sp. nov. (fig. 10). Urediis amphigenis, sparsis vel aggregatis, pulverulentis, cinnamomeo-brunneis, ellipticis vel linearibus, 0.4–1.5 mm. longis vel confluentibus, paraphysibus nullis; urediosporis ellipticis vel obovoideis, 18–22 (–24) × (22–) 24–27 (–30) μ, membrana (1.5–) 2–2.5 μ cr., echinulata, cinnamomeo-brunnea, poris germ. 5–7 sparsis. Teliis urediis conformibus sed in vaginis culmisque evolutis, pulvinatis, atro-brunneis; teliosporis plerumque ellipsoideis, vel clavato-ellipsoideis, 19–25 × (27–) 30–36 (–38) μ, membrana 2.5–3.5 (–4) μ ad apicem 4–6 μ cr., intense

rufo-castanea, levi; pedicello flavo-brunneo, plus minusve crasse tunicato, usque ad 65 μ longo, persistenti.

On *Perotis indica* K. Schum., Newton, Sierra Leone, Jan 17, 1950, *F. C. Deighton 3464* Type: (A.H., C.M.I.), Accra and Aburi Gold Coast, Dec. 10, 1953, *Deighton 5445, 5446.*



FIGS. 11–17. FIG. 11. Teliospores of *Puccinia pappophori.* (From type.) FIG. 12. Teliospores of *Puccinia saltensis.* (From type.) FIG. 13. Teliospores of *Uromyces nasellae.* (From type.) FIG. 14. One teliospore and one urediospore of *Puccinia hyparrheniicola.* (From type.) FIG. 15. Teliospores of *Uropyxis wiehei.* (From type.) FIG. 16. Teliospores of *Uromyces snowdeniae.* (From type.) FIG. 17. Teliospores of *Uromyces sporoboloides.* (From type.) × 800.

The few telia seen were on the leaf sheath.

P. perotidis is generally similar to *P. aegopogonis* Arth. et Holw. but has larger uredia, more deeply pigmented and thicker-walled urediospores, and larger and more intensely pigmented teliospores.

Puccinia saltensis sp. nov. (fig. 12). Urediis epiphyllis, sparsis, cinnamomeo-brunneis, pulverulentis, ellipticis, 0.2–0.5 mm. longis, paraphysibus aureis vel flavo-brunneis, capitatis 13–26 μ latis, usque ad 90 μ longis, membrana plus minusve uniformiter 2.5–4 μ cr.; urediosporis plerumque ellipsoideis vel late ellipsoideis, 16–20 × 18–25 (–27) μ, membrana intense cinnamomeo-brunnea, minuteque echinulata, 1.5–2 (–2.5) μ cr., poris germ. (4–) 5 vel 6 sparsis. Teliis urediis conformibus sed atro-brunneis et compactis; teliosporis ellipsoideis, oblongo-ellipsoideis, vel clavatis, ad apicem plerumque rotundatis, deorsum plerumque contractis, medio leniter constrictis, (14–) 16–19 (–23) × (30–) 33–46 (–50) μ, membrana castaneo-brunnea, 1.5–2.5 (–3) μ cr. ad apicem (5–) 7–9 (–11) μ cr., levi; pedicello persistenti, aureo- vel flavo-brunneo, tenuiter tunicato, usque ad 55 μ longo.

On *Stipa tucumani* Parodi, Prov. Salta, Argentina, May 2, 1942, *Hunziker 1844* Type: (A.H., U.S.D.A.). Specimen from the grass collections of the U. S. National Herbarium.

In South America occur also *P. digna* Arth. et Holw., *P. nasellae* Arth. et Holw. and *P. entrerriana* Lindq. on *Stipa*. While both *P. digna* and *P. nasellae* have capitate paraphyses the urediospores are larger and paler. *P. entrerriana* lacks paraphyses and has three equatorial pores. *P. oligocarpa* Syd. et Butl., also with uredial paraphyses, has covered telia and teliospores with short pedicels. *P. saltensis* is thus distinct from other rusts of *Stipa* and related genera.

Uromyces nasellae sp. nov. (fig. 13). Urediis epiphyllis, sparsis vel seriatim dispositis, pulverulentis, flavidis, ellipticis, 0.5–1.5 mm. longis, paraphysibus nullis, epidermide rupta conspicue; urediosporae ovatae vel ellipsoideae, (21–) 23–26 (–28) × (28–) 30–35 (–38) μ, membrana 2.5 μ cr., hyalina, echinulata, poris germ. obscuris, verisimiliter 10–13 sparsis. Teliis urediis conformibus sed pulvinatis, atro-brunneis; teliosporis obovoideis, ovatis vel oblongo-ellipsoideis, (19–) 21–24 (–26) × (27–) 30–36 (–40) μ, membrana 2–3 μ cr. ad apicem 5–8 μ cr., castaneo-brunnea, levi; pedicello flavo-brunneo, crasse tunicati, persistenti, usque ad 70 μ longo.

On *Nasella pubiflora* (Trin. et Rupr.) Desv., La Paz, Bolivia, Mar. 26, 1920, *E. W. D. & Mary M. Holway 464* Type: (A.H.) (Reliq. Holw. No. 72 as *Uromyces pencanus* (Diet. et Neger) Arth. et Holw.), Mar. 27, 1920, *Holway 476*.

U. nasellae is not similar to *U. pencanus*, which has smaller cinnamon-brown urediospores and smaller teliospores, but is nearer to *U. fuegianus* Speg. on species of *Festuca*. *U. fuegianus* also has hyaline urediospores which are broader (25–33 μ) and teliospores which are deep golden-brown rather than chestnut.

Uromyces snowdeniae sp. nov. (fig. 16). Urediis amphigenis vel plerumque hypophyllis, sparsis vel laxe aggregatis, ellipsoideis, 0.3–1.3 mm. longis, flavidis, pulverulentis, paraphysibus nullis; urediosporis late ovatis vel plus minusve globoideis, 15–18 × 17–20 μ, membrana 1–1.5 μ cr., hyalina vel pallide flavida, echinulata, poris germ. obscuris, 5–7 sparsis. Teliis plerumque hypophyllis, erumpentibus, pulvinatis, atrobrunneis, ovatis vel oblongis, 0.3–1.0 mm. longis, frequenter confluentibus; teliosporis plerumque plus

minusve obovoideis, (16–) 18–20 (–22) × (21–) 23–27 μ, membrana 2–2.5 μ cr. ad apicem 3.5–5.5 μ, castaneo-brunnea, levi; pedicello flavidulo, tenuiter tunicati, persistenti, usque ad 45 μ longo.

On *Snowdenia polystachya* (Fresen.) Pilger, Aruba Sea, Abyssinia, Oct. 2, 1862, *Schimper 1028*, on *S. scabra* (Pilger) Pilger, Bahati Forest, Kenya, Oct. 3, 1951, *A. Bogdan 3272* Type: (A.H., Kew).

U. snowdeniae is one of a group of four small-spored and generally similar species all of which have urediospores averaging less than 23 μ in length and teliospores averaging less than 27 μ in length. The other three are *U. kenyensis* Hennen on *Chloris*, *U. minimus* J. J. Davis on *Muhlenbergia*, and *U. aegopogonis* Diet. et Holw. on *Aegopogon*. These three have teliospores with the apical wall 5–8 μ in thickness.

No other rust has been recorded on the tribe Arthropogoneae.

Uromyces sporoboloides sp. nov. (fig. 17). Urediis plerumque amphigenis, sparsis vel laxe aggregatis, pulverulentis, flavo-brunneis, ellipticis, 0.5–2.0 mm. longis, epidermide rupta conspicue, paraphysibus nullis; urediosporis ovatis vel late obovoideis, (19–) 21–26 × (24–) 26–33 (–35) μ, membrana 1.5–2.5 μ cr., aureo- vel cinnamomeo-brunnea, echinulata, poris germ. 4, equatorialibus. Teliis plerumque hypophyllis, sparsis vel aggregatis, atro-brunneis, subepidermalibus, indehiscentibus vel tarde nudis, paraphysibus aureis coalitis praeditis, plus minusve loculatis ellipticis vel elongatis, 0.3–1.5 mm. longis; teliosporis variabilibus, angulariter obovoideis, ad apicem frequenter truncatis, (16–) 20–26 (–29) × (25–) 29–33 (–36) μ, membrana castaneo-brunnea, 1.5–2.5 μ cr. ad apicem 3.5–5 μ cr. et obscuriore, levi; pedicello flavidulo, tenue tunicati, persistenti, usque ad 30 μ longo.

On *Sporobolus berteronianus* (Trin.) Hitchc. et Chase, Riobamba, Ecuador, Aug. 10, 1920, *E. W. D. & Mary M. Holway 862* Type: (A.H.) (Reliq. Holw. No. 98 as *Uromyces sporoboli* Ell. et Ev.), Quito, Ecuador, Aug. 15, 1920, *Holway 898*, La Paz, Bolivia, Mar. 29, 1920, *Holway 481*, Cochabamba, Bolivia, Mar. 1, 1920, *Holway 351* (Reliq. Holw. No. 54 as *U. sporoboli*), Panamavida, Chile, Oct. 14, 1919, *Holway 228*.

This species differs markedly from *Uromyces sporoboli* Ell. et Ev. because of the long-covered telia. Other species which have long-covered or tardily dehiscent (but aparaphysate) telia, echinulate urediospores with equatorial pores, and aparaphysate uredia are *U. microchloae* Syd. on *Microchloa*, *U. dactyloctenii* Wakef. et Hansf. on *Dactyloctenium*, *U. tenuicutis* McAlp. (*U. ignobilis* Syd., *U. wellingtonica* T. S. et K. Ramak.) on *Sporobolus*, *U. leptodermus* Syd. on numerous genera of Paniceae, and *U. trichoneurae* Doidge on *Astrebla*, *Trichoneura* and *Tripogon*.

Uropyxis wiehei sp. nov. (fig. 15). Urediis incertis; urediosporis late ovoideis vel globoideis, 17–19 × 19–24 μ, membrana 2.5–3 μ cr., flavida, minuteque echinulata, poris germ. obscuris, sparsis, verisimiliter 6–8; paraphysibus peripheralibus (?) incurvatis, hyalinis vel flavidis, 10–15 × 40–60 μ, membrana in parte interiore 1–2 μ cr., exteriore 3–6 μ cr. Teliis caulicolis plerumque in incrassationibus leniter fusiformibus usque ad 5 cm. longis

confluentibus, obscure cinnamomeo-brunneis vel castaneo-brunneis; teliosporis ellipsoideis, utrinque rotundatis, medio non constrictis, (26–) 28–33 (–35) × (38–) 40–48 (–51) μ, membrana bilaminata, parte exteriore hyalina 0.5–2 μ cr., interiore castaneo-brunnea vel obscure cinnamomeo-brunnea, 3.5–5 μ cr., minuteque echinulata vel apparenter levi, quaque cellula poris germ. 2 equatorialibus instructa; pedicello hyalino, crasse tunicato, 4–5 μ lato, usque ad 160 μ longo, persistenti.

On stems of *Aeschynomene abyssinica* Vatke (= *E. rueppelii* Baker?), Dedza, Nyasaland, Sept. 4, 1950, *P. O. Wiehe 861* Type: (A.H., C.M.I.), Cholo, Nyasaland, Aug. 12, 1950, *Wiehe 826*.

This is the first species of *Uropyxis* to be recorded on species of *Aeschynomene*. An accurate descriptio of the uredia is impossible with these collections.

THE ARTHUR HERBARIUM, PURDUE UNIVERSITY AGRICULTURAL EXPERIMENT STATION, LAFAYETTE, INDIANA

BULLETIN OF THE TORREY BOTANICAL CLUB

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TORREYA

Biological Transmission of Plant Viruses by Insect Vectors[1]

KARL MARAMOROSCH

Most vectors of plant virus diseases are arthropods of the families Aphididae (aphids), Cicadellidae (leafhoppers), and Aleyrodidae (white flies). A few viruses are transmitted by members of other families like Coccidae (mealybugs), Thysanoptera (thrips), and Acarina (mites). Two major types of virus-vector relationship are usually recognized. Vectors of one type acquire a virus in short feeding periods and transmit it almost immediately. In every known case such vectors soon lose the virus. Vectors of the second type generally acquire virus by feeding for somewhat longer periods on infected plants. In contrast to the first type, these vectors are unable to transmit virus to healthy plants immediately. An incubation period of considerable length occurs between the time of acquisition of virus and the time of its transmission to a susceptible host. Only after an incubation period of many hours, days, or even weeks, do vectors of this type become infective. Plant viruses are retained by such vectors for considerable lengths of time, often for the remainder of their lives, without need of replenishment from infected plants. The virus-vector relationship in this case represents a highly specialized adaptation of the virus to the arthropod host. This obligatory relationship between the vector and the transmitted virus is indicated by a high degree of specificity; in the majority of cases one or a few closely related species are found to transmit a given virus. This relationship is often called *biological* and the transmission is then known as *biological transmission*.

Excellent evidence presented by a number of workers in the past two decades has established beyond reasonable doubt that several plant viruses multiply in their arthropod vectors. The first experimental evidence of plant virus reproduction in insect vectors came from the work of Fukushi in Japan in the years 1935 to 1939. After it was found that the rice-stunt virus passed through the eggs of infective females of *Nephotettix apicalis* to the progeny, Fukushi demonstrated that virus from a single female could be passed through the egg to 6 succeeding generations without replenishment from plants. It is quite likely that the actual dilution of the original virus, attained by Fukushi in the sixth generation, surpassed 10^{-8}. However, ability of the insects to infect plants showed no progressive decline during successive generations.

The relationship of aster-yellows virus to its vector *Macrosteles fascifrons* is probably the best known virus-vector relationship in the group of biologically transmitted viruses. The first experimental evidence that aster-yellows virus multiplies in its vector was presented by Kunkel in 1937. Heat treatment was used for inactivation of the virus in infective vectors and it was found that the insects regained ability to transmit yellows if treatment at 36° C. lasted 11 days or less. However, the heat-induced incubation periods were progressively longer with longer exposures to high temperatures. It was postulated that during the heat-induced incubation period that portion of the virus not inactivated by the treatment multiplied sufficiently to render the insects infective. It was also shown that the heat treatments were affecting the virus and not the insects. Leafhoppers that lost their transmitting ability through long heat treatments could readily be rendered infective by letting them feed again on diseased plants.

Further evidence that aster-yellows virus multiplies in its insect vector came from experiments by Black, who in 1941 presented data on measurements of virus increase in insects during incubation. These data indicated multiplication of the virus in the insects at least a hundredfold between the 2nd and 12th days of the incubation.

In 1952 the mechanical inoculation technique of insect vectors was applied by

[1] Paper presented before the Torrey Botanical Club, December 6, 1955.

Maramorosch in a serial passage experiment and the virus carried serially through 10 groups of leafhoppers. It was calculated that the virus would be diluted approximately to 10^{-4} at each passage and that it would become less concentrated in successive passages unless it multiplied in the insect. The dilution of original virus used for injection in the 10th passage would have reached 10^{-40}, yet tests indicated that there was just as much virus present at this passage as in the 1st passage. The successful inoculation, therefore, attained in the 10th passage with a final dilution of 10^{-40} in terms of the original virus provided conclusive evidence that the virus had multiplied in the insect. In these tests all inoculated insects had access to living plants. Recently a new method of measuring virus increase by use of insect tissue cultures was developed. This technique eliminated the need for living plants or plant material. Aster leafhoppers were artificially infected and 2 days later cut into pieces. Small bits of insects were kept in sterile conditions for 10 days in drops of a suitable nutrient solution containing sugar, mineral salts, amino acids, bovine albumin, and antibiotics. Afterwards an inoculum prepared from these insect tissues was injected into virus-free aster leafhoppers by means of a semi-automatic microsyringe. Although virus could not be recovered immediately after the insects were cut into pieces, it was recovered from these bits of tissue after 10 days. The tests demonstrated that aster-yellows virus completed its incubation in tissues of the vector in the absence of plant tissues.

In 1944 Black found that clover club-leaf virus passes through the egg of its vector, *Agalliopsis novella*, to a high proportion of the progeny. Serial passage of this virus through 21 generations of vectors was begun in 1945 and was continued for more than 5 years. Infectivity was retained throughout the experiment. Thus it was demonstrated that the virus can be maintained essentially indefinitely in its insect vector. The dilution of the original virus exceeded $1:2.8\times10^{26}$ on a conservative estimation. In 1955 clover club-leaf virus was mechanically transmitted to clover leafhoppers (Bull. Torrey Bot. Club **82**(5): 339–342). The incubation period in injected insects was comparatively long, which indicated a rather slow multiplication of the virus in its vector.

The fourth virus shown to multiply in its vector was the wound-tumor virus. Convincing evidence for its multiplication in the insect *Agallia constricta* was obtained in 1952 by Black and Brakke who applied the needle inoculation technique for the mechanical transmission of the virus to insects. Eventually the original virus was diluted to approximately 10^{-18}, in 7 passages, without loss of infectivity although in actual dilution tests wound-tumor virus was never recovered from insect juices at dilutions beyond 10^{-5}.

The fifth virus carried from insect to insect in serial passages was the corn-stunt virus in *Dalbulus maidis*.

There is no reason to assume that the number of viruses in this category is limited to the 5 that have been studied in detail. Nor is there any reason to suspect that multiplication of plant viruses is limited to vectors among the Cicadellidae. Very likely many other plant viruses that are transmitted biologically also multiply in their respective vectors. The evidence presented over the past 20 years has a bearing on our ideas, not only of virus multiplication but of classification and origin. These viruses cannot be considered as plant viruses only. They constitute a close link between plant and animal viruses. The ability to multiply in such diversified hosts as plants and animals strongly suggests that they are parasitic organisms. The hypothesis of a large molecule precursor responsible for virus multiplication can hardly account for multiplication of the "plant-animal" viruses. It is unlikely that such a large molecule precursor would occur in two hosts that are serologically and otherwise so unrelated. The morphology of viruses transmitted by leafhoppers shows that they are complex in their nature. Presumably some virus particles are surrounded by a membrane. Their morphology and the complex biological behavior seem to place them in the category of microorganisms. These viruses mutate and their mutations can be induced by physical means like mutations in larger microorganisms. Multiplication is an intrinsic

character of a functional organism in which like produces like. Viruses, probably, are unable to sustain independent metabolism and in this characteristic may represent an extreme form of parasitism. Retrograde evolution may explain the existence of the highly specialized plant-virus-arthropod relationship of biologically transmitted viruses. The viruses do not interfere with the life functions of their animal vectors. Should the viruses in some way endanger the life span of arthropod vectors or interfere with their feeding, opportunities to transmit the infective agent would be diminished. Is it proper to apply the term *vector* to arthropods and the term *host* to plants? If we look at the problem from the standpoint of disease in plants, the arthropods play merely the role of carriers. But from the virus aspect and its requirements for survival in nature, the arthropods constitute better hosts or reservoirs than the plants.

The life cycles of viruses, alternating between plants and arthropods, could have arisen either by very simple nutritive requirements or by a well organized adaptation of all metabolic activities. Our present knowledge of biologically transmitted plant viruses shows that, with certain exceptions, they have a fairly large host range among plant species but a narrow one among the arthropod vectors. This favors the assumption that their adaptation to the animal host is well organized and, from an evolutionary point of view, probably also of much longer existence. It, therefore, seems conceivable that such viruses were originally arthropod viruses and, because of the long association between the host and parasite, became ideally balanced in a symbiotic relationship. This explanation could account for the complete tolerance of the otherwise highly virulent plant viruses in respect to the "susceptible" arthropods.

This view of the origin of biologically transmitted viruses in arthropods seems further supported by the finding that several viruses have the capacity of passing through the egg of the vector to the progeny and of being thus maintained indefinitely in animals without the necessity of alternating plant hosts. Others are only occasionally transmitted transovarially, and still others have to rely on the complicated life cycle imposed by alternation between plants and arthropods.

Biologists often tend to think of viruses as being organisms, just as chemists tend to think of them as being chemicals. There is no reason to assume that all viruses, or even all viruses causing plant diseases, multiply in a similar fashion. In some fungi a great variety of developmental stages occurs, some being sexual and others asexual. In certain highly developed groups, such as rusts, there are life cycles alternating between different and highly specific plant hosts. It seems reasonable to assume that various groups of viruses, like different groups of fungi, multiply differently from each other; for instance, tobacco-mosaic virus may multiply in an entirely different way from that characteristic of aster-yellows virus. The recent crystallization of poliomyelitis virus suggests that animal and plant viruses are basically very similar. The finding that influenza virus consists mainly of ribonucleic acid and not, as was assumed for all animal viruses, of desoxyribonucleic acid, also points to the similarities between plant and animal viruses.

Evidence for the existence of a group of viruses that are able to multiply both in plants and animals and that require both hosts for their maintenance in nature has been well established. The still prevailing and very convenient division of viruses into bacteriophages, animal, plant, and insect viruses may have to be abandoned in the future; like bacteria, which no longer are divided according to the hosts they attack, viruses will come to constitute a unified field of study.

THE ROCKEFELLER INSTITUTE FOR MEDICAL RESEARCH,
NEW YORK, N. Y.

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Book Reviews

Landscaping Your Own Home. By Alice L. Dustan. vi + 374 pages; Figs. 21, plates 24 + 1 colored. The Macmillan Company, New York, 1955. $3.95.

Practicality would probably be the best descriptive word to use for this book for do-it-yourselfers in the development of a domestic landscape. A few general hints are given on basic principles of design and composition and more are scattered at appropriate places in the text; but much of this is left to the judgement and taste of the home owner. Starting with an inventory of the site and its assets, a basic plan is developed, taking into account the family way of living. Such things are considered as the divisions of the property, the retention of trees on a wooded lot, the selection and location of trees, shrubs, and other plants, the desirability of fruit trees, the location of a swimming pool. Precise directions for planting, with helpful lists in appropriate places, emphasizing ecological relationships. Year round color effects have good treatment, and the relative merits of deciduous and evergreen plants. Maintenance is well handled.

Construction of necessary garden elements—wood, masonry, concrete,—is given a place. For example, steps may be uncomfortable to use, so suitable formulae are given as to the relation of riser to tread.

The writing is sprightly and leaves no doubt of authority. The illustrations are well selected, with a number of before and after views with plans. The book can be of inestimable value in avoiding mistakes, or of solving them if they should be made.—Charles H. Connors, Rutgers University.

The Genus Phlox. By Edgar T. Wherry. 174 pages. Morris Arboretum Monographs. III. 1955. $4.00.

The present monograph is the culmination of Dr. Wherry's thirty years of study of *Phlox*, and represents his magnum opus. It includes keys, full descriptions, full synonymy with literature-citations, numerous drawings and photographs, explanatory comments, and stippled distribution-maps. The only specimens cited are the types of recognized taxa, and it should be noted that the dots on the maps do not represent individual collections or stations. Sixty-seven species (3 of them newly described) are distributed among three sections and eighteen subsections. Many of the species are considered to consist of several subspecies each, and a total of 123 ultimate taxa (subspecies and undivided species) is recognized. Most of these have been studied in the field as well as in the herbarium by Dr. Wherry, very often at the type localities as well as elsewhere.

The keys to the taxa of each subsection are inserted separately in the text, are of non-indented form, and follow the novel principle of referring to numbered ultimate taxa without regard to whether these are species or subspecies. Each ultimate taxon is fully treated according to a uniform plan, but species which are considered to consist of two or more subspecies are not provided with a separate specific description or other treatment.

The depressed phloxes, constituting the section Microphlox, form a particularly difficult taxonomic complex, and other botanists may have trouble with the keys in this section. Having recently attempted to treat some of these same species for a flora, the reviewer doubts that a wholly satisfactory key could be provided for them in any case, and an attempt to expand the specific limits beyond those seen by Dr. Wherry tends to confuse rather than clarify the taxonomy of this group.

Within the framework of his taxonomic philosophy, Dr. Wherry has presented a clear and consistent treatment, based largely on classical taxonomic methods. A notable feature of his philosophy, which he has expressed in personal conversation as well as in print, is a desire to provide nomenclatural recognition for morphologic variation, coupled with a reluctance to reduce any published name to outright synonymy. Those botanists who think of subspecies (or varieties) as self-perpetuating natural populations which are geographically or ecologically marked within the species as well as being morphologically recognizable, have often found that Dr. Wherry's subspecies do not meet their criteria. The present work will be no exception in that regard, although a number of names have been disposed of as representing morphologic varients which are not accorded formal taxonomic status.

Dr. Wherry's species in *Phlox* are more likely to meet with general acceptance than his subspecies. Closer attention to the geographic factor might have sharpened the specific lines in some instances, but so far as the reviewer's experience goes, the species recognized in this monograph generally *do* represent self-perpetuating, morphologically recognizable populations with geographic-ecologic coherence, and the reviewer is convinced that most of these would be recognized as a species by any other monographer of the genus.—ARTHUR CRONQUIST, New York Botanical Garden

Gesetzmässigkeiten der Gestaltwandlung im Blütenbereich Ihre Bedeutung für das Problem der Evolution. By Erich Nelson. i–xii + 302 pp. Figs. I–IV (colored) V–XIV (b & w). 1954. Published by E. Nelson, Chernex-Montreux (Switzerland). 81.10 fr. (Swiss) = $19.00.

This beautiful, informative and provocative volume was published by the author with support from the Swiss National Fund for the Advancement of Scientific Research. That this assistance was afforded the author indicates the very high level of attainment of the work.

Nelson's interest in morphogenetic and phylogenetic problems was fixed during the years of study that he devoted to the Orchidaceae of middle Europe. In 1931 he published a monographic study of this group and in succeeding years turned his attention to a study of morphogenetic problems in flowering plants in general. The phylogenetic implications of morphological variations observed in relict groups studied by the author during travels through southern Europe, the Mediterranean area and western Asia were compiled during the pre-World War II days. During the period from 1944–54 the author, working at the Geobotanical Forschungsinstitut Rübel in Zurich, had an opportunity to correlate his observations with those contained in the earlier literature. This is evidenced by a bibliography of approximately 390 entries (the great majority to publications in German). The author, making use of his unique experiences and opportunities, has brought together a mass of well organized information and many theories of interest to students of floral anatomy and morphology, taxonomy, ecology, genetics and plant geography.

The volume is divided into four parts. In general, the first part concerns itself with the physiological determination of number and position of the floral members. Topics here range from terminal and lateral position effects and the physiological

relationships between the whorled and spiral arrangements to a chapter discussing the genotypic fixation of numerical relationship. The second part discusses secondary changes in the floral reproductive organs and their importance in the final form and structure of the flower. A variety of chapters discuss physiological and germinal factors as determiners in floral morphology and the origin and regularity of the corolla structures. Direct reference is made to conditions found in a number of families and individual species. The third section is concerned with the bilaterally symmetrical flower and traces controlling factors from the vegetative structure through various types of dorsi-ventral flowers. Again the discussions are supported by direct reference to numerous examples.

The fourth section discusses a number of theoretical considerations in floral morphology based mostly on the theory of natural potential.

Although much of this study is compendious, there is a large core of observations that are original with the author. I cannot escape the conclusion that Nelson's greatest contribution has been the careful organization of a tremendous mass of information in such a manner as to allow a critical analysis of the morphogenetic theories. This volume is the product of more than twenty years of research, and it will probably take an equal period of time to appreciate its full content and value. Certainly a number of the questions raised by Nelson will be answered only by extensive experimentation and descriptive research.—HARRY K. PHINNEY, Department of Botany, Oregon State College, Corvallis, Oregon.

Embryogenesis in Plants. By C. W. Wardlaw. ix–381 pages. 84 figs. Methuen and Co. London. 1955. $7.00.

Three noteworthy textbooks have appeared in the field of plant embryology during the last five years: Plant Embryology by D. A. Johansen (Chronica Botanica Co., 1950), An Introduction to the Embryology of Angiosperms by P. Maheshwari (McGraw-Hill, 1950) and Embryogenesis in Plants by C. W. Wardlaw (Methuen and Co., 1955). Dr. Johansen has critically reviewed the literature and described and illustrated the stages of embryological development in the investigated families of seedplants. Emphasis throughout has been on comparative morphology with particular attention devoted to the typing of embryos and to embryological laws. Professor Maheshwari has considered the several types of angiosperm embryos and in addition has treated such allied subjects as the microsporangium, megasporangium, female gametophyte, male gametophyte, fertilization, endosperm, apomixis, polyembryony, embryology in relation to taxonomy and experimental embryology.

Professor Wardlaw's text differs from the above in that he covers the algae, bryophytes, pteridophytes and seedplants and in the emphasis placed on the techniques of physiology and genetics in embryological investigations. While recognizing the importance of amassing morphological data, he would shift emphasis from morphology to the process of embryogeny. An innovation, and one for which there is ample justification, is his belief that the field of embryology would be enriched by extending it to include not only development from fertilized eggs but from spores as well. This makes possible very effective comparison of early growth of the sporophyte and gametophyte in the algae, bryophytes, and vascular plants.

Two chapters are devoted to factors in embryogenesis and one to general conclusions; these contain the most stimulating and significant contributions made by Professor Wardlaw. A well-chosen survey is made of embryology in the Algae, Bryophyta, Psilotales, Equisetales, Lycopodiales, Filicales, Gymnospermae and Angiospermae. Trends within and between these groups are clearly set forth in terse descriptions and in a discriminating selection of illustrations from the literature. Attention is given to phylogenetic relationships and an attempt is made to explain observed phenomena in terms of biochemistry and genetics so that our knowledge of form and structure will not remain as so much descriptive data. Systematists are wisely counseled that the factors underlying the process of embryogeny ". . . must be more fully explored before embryological data can be used with safety in taxonomy and phylogeny."

The egg and zygote are considered as dynamic biological systems from which the

specific patterns responsible for embryogenesis are early established. The basic problem, therefore, becomes that of identifying the kind and role of gene controlled processes in embryogeny and to discover the part played by polarity, diffusion gradients, surface tension, light, gravity, reciprocal relationship of parts, and other factors involved in development. Progress in this direction has been made although it falls far short of that made by zoologists in animal embryology. The biochemical approach is without question the outstanding feature of Professor Wardlaw's text.

The book is attractively printed and freely illustrated with some eighty full-page plates of line drawings. The bibliography contains 737 citations.—M. A. JOHNSON, Department of Botany, Rutgers University.

NOTES

Two New Indices Important to Botanists

Ecology Thirty-Year Index (Volumes 1–30, 1920–1949). This index was prepared by a committee of the Ecological Society of America consisting of Dr. John M. Aikman and Dr. Frank C. Gates with the co-operation of 25 other members of the Society. Mrs. D. B. Lawrence edited the final manuscript and prepared it for publication. The index is not separated into author and subject matter but is integrated as a single alphabetically arranged listing. There are 212 pages. It may be obtained from the Business Manager of ECOLOGY, Dr. H. J. Oosting, Box 6875, College Station, Durham, N.C. ($4).

Index to the Bulletin of the Torrey Botanical Club (Volumes 1–75, 1870–1948). This index was compiled by Dr. H. W. Rickett. It includes a 108-page index to authors, plus an 886-page index to subject matter including names of plants. Publication of the index was made possible by a grant from the National Science Foundation. The book may be ordered from the Business Manager of the Torrey Botanical Club, Dr. R. M. Duffy, New Jersey State Teachers College, Jersey City 5, N. J. ($15).—M. F. BUELL

The Annual Meeting of the Club Was held at Hunter College on January 17. Professor Elva Lawton, retiring president, addressed the meeting with a resume of her field experiences during the summer of 1955. The following officers were elected:

President, Lela V. Barton
1st Vice-President, Edwin T. Moul
2nd Vice-President, David D. Keck
Corresponding Secretary, Eleanor Witkus
Recording Secretary, Frank G. Lier
Treasurer, Gily E. Bard
Editor, Charles A. Berger
Business Manager, Regina M. Duffy
Bibliographer, Lazella Schwarten
Chairman of Field Committee, David E. Fairbrothers
Representative on the Board of Managers of the New York Botanical Garden, P. W. Zimmerman
Representatives on the Council of the A.A.A.S., A. E. Hitchcock, Lindsay S. Olive
Delegate to the New York Academy of Sciences, Annette Hervey

Elected members of the Council are:

1954–1956

William Crotty
Regina M. Duffy
Edwin B. Matzke
J. Herbert Taylor

1955–1957

John A. Small
David D. Keck
George L. McNew
Joseph E. Schuh

1956–1958

Honor Hollinghurst
Peter Nelson
Sam F. Trelease
Robert H. Whittaker

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INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

TAXONOMY, PHYLOGENY AND FLORISTICS

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